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Spiders of the Oriental-Australian region. III. Tetrablemmidae, with a world revision

PEKKA T. LEHTINEN

Lehtinen, P. T. 1981: Spiders of the Oriental-Australian region. III. Tetrablemmidae, with a world revision. — Acta Zool. Fennica 162:1—151.

Spider families Pacullidae and Tetrablemmidae are taxonomically revised and united into a single family that is placed into Sicarioidea.

Two male/female copulatory locking systems are described; they are not known outside Tetrablemmidae. Paired copulatory orifice is found in females of *Paculla* and *Sabahya*. The tetrablemmid web is described: a small dense sheet along the surface of dead leaves. Ecological data is given for 52 species collected by the author.

The taxonomic value and evolution of different structural characters is discussed, and a cladogram of all genera is presented. The vulval structure is the best diagnostic character above the species level in female tetrablemmids and the type of sexual dimorphism of chelicerae and carapace for males.

The subfamily Pacullinae consists of two tribes, Peraniini (*Perania* and *Mirania* gen. n.) and Pacullini (*Paculla*, *Lamania* gen. n., and *Sabahya*), and a total of 15 named species, including a new species both from Borneo and from Malaya.

The subfamily Tetrablemminae consists of five tribes: Fallablemmi (*Afroblemma* gen. n. and *Fallablemma*), Brignoliellini (*Indicoblemma*, *Chavia* gen. n., *Choirolemma*, *Singaporemma*, *Pahanga*, *Borneomma*, and *Brignoliella*), Ablemmi (*Ablemma* and *Sulaimania* gen. n.), Tetrablemmi (*Shearella* gen. n., *Mariblemma* gen. n., *Gunasekara* gen. n., *Singalangia* gen. n., *Tetrablemma*, *Rhinoblemma* gen. n., *Cuangoblemma*, and *Anansia* gen. n.), and Mattini (*Matta*, *Micromatta* gen. n., *Caraimatta* gen. n., and *Hexablemma*). *Monoblemma* and *Maijana* gen. n., are left as Tetrablemminae incertae sedis. Tetrablemminae consists of 93 known species, 42 of them described here as new (Ceylon 4, India 1, Nepal 1, Thailand 2, Vietnam 3, West Malaysia 3, Sumatra 5, Borneo 8, Celebes 6, Java 1, Flores 1, Luzon 2, Mindanao 1, New Guinea 2, Fiji 1, and Mexico 1). The genera *Borneomma*, *Brignoliella*, *Ablemma*, and *Tetrablemma* are divided into subgenera, including five new. New subspecies are described in three species, including the type-species of the family. Another sex is described for six species, previously known only by one sex. Among them are the type-species of the family, *Tetrablemma medioculatum*, and the first female for *Paculla*, type genus of Pacullinae.

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Helsinki 31.12.1981 Helsingfors

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1. Introduction

Spider material collected by the tropical expeditions of the Zoological Museum of Turku University into the Oriental-Australian region (1969—1979) is treated in a series of revisionary papers. For other, completed parts, see Lehtinen & Hippa (1979) and Lehtinen & Saaristo (1980). Most of the spider material of these expeditions was collected by the author.

Tetrablemmidae, including Pacullidae, are known as armoured spiders because of the complicated patterns of their abdominal scuta. They have long been among the most poorly known groups of spiders, and only ten years ago very few specimens of tetrablemmids were available in museums. There are no published figures for most of the species described in the last century. The increase in known tetrablemmid taxa during different periods of taxonomic activity is summarized in the table below. The numbers refer to valid taxa only, numbers in parentheses to Oriental-Australian taxa, including those from the Seychelles Islands. Other sexes which have been described later are listed last.

Only two synonyms of tetrablemmid species are established here, both of them in the paculline genus *Perania*, and no previously known synonyms are presented. Tribes, subgenera, and subspecies have not been suggested in previous papers on Tetrablemmidae. In this paper these auxiliary categories are sparingly

used wherever they give more accurate information.

Roewer (1963a, b), Komatsu (1968), and Brignoli (1972a, b, 1973) discussed the relationships between various tetrablemmine genera and their affinities to pacullids. They also finally removed tetrablemmids from Theridiidae, where most of the species had been catalogued. The placing into Oonopidae or Hadrotarsidae (Petrunkévitch 1928 & others, Roewer 1963a, b) was carried out on the simple basis of the strong sclerotization of the abdomen. Brignoli (1973) first placed all Tetrablemmidae and Pacullidae close to each other as a monophyletic group of Haplogyne spiders, but he was misled by the fact that all specimens available to him belonged to Tetrablemmidae s. str. (= Tetrablemmiinae).

The present study was already complete at the beginning of 1978 (with regard to material collected then), when I was informed of the parallel study of Shear (1978), then in press. The material of Shear as well as my own material from 1978—79 was later added. When this paper was already in press, I received information about three additional papers on Tetrablemmidae. As it became evident that these smaller papers would be published before this world revision, the names originally used in this paper were

	Genera		Species	
	Pacullinae	Tetrablemmiinae	Pacullinae	Tetrablemmiinae
1873—98	2 (2)	1 (1)	5 (5)	4 (4)
1920—68	—	4 (1)	—	12 (8)
1972—80	1 (1)	8 (7)	8 (8)	35 (21) + 1
This paper	2 (2)	12 (8)	2 (2)	42 (41) + 4
Known taxa	5 (5)	25 (17)	15 (15)	93 (74)
Whole family	29 (22)		108 (89)	

changed to the names suggested by Bourne (1980) and Deeleman-Reinhold (1980) for taxa described by two of us in order to avoid unnecessary synonyms. *Sabahya kinabaluana*, *Borneomma roberti*, and *Ablemma circumspectans* were described from the same locality in Malaysian Borneo by Deeleman-Reinhold (1980) and by the present author, while *Indicoblemma sheari* and *Tetrablemma loebli* were described, again from exactly the same localities, in the Kumaon and Darjeeling regions of the Indian Himalayas by Bourne (1980) and by the present author. Deeleman-Reinhold's paper could not be taken into account in detailed discussions as changes in the text have had to be kept to a minimum.

At this moment, the type material of all old, insufficiently described species has been checked by myself, or, in the case of a few exceptions, by Shear or Brignoli. In these cases, they have published good drawings of the types, allowing unambiguous identification and placement of these species. *Tetrablemma okei* and *Phaedima armata* have been studied according to fresh topotypical material only, while the status of *Paculla birmanica* could not be checked using extant specimens.

Intraspecific variation of Tetrablemmidae has been carefully studied by me only with regard to the Old World species, and thus no new taxa are suggested for deviating populations of some Neotropical species mentioned by Shear (1978).

Shear (1978) treated Pacullidae and Tetrablemmidae as independent families, but according to my standards (Lehtinen 1978) they doubtless constitute a single family, comparable to any recently revised and delimited spider family e.g., Theridiidae, Anyphaenidae, or Lycosidae. Before Shear's paper there have been no generic standards whatsoever in existence, but he nevertheless included members of different tribes into a single genus (*Monoblemma*, *Tetrablemma*), sometimes with notes on possible polyphyly of his taxa (*Monoblemma*). Shear also presented a cladogram with preliminary discussion about the evolution of different structural characters, and although I largely disagree with his argumentation and resulting classification his paper represents

enormous progress in our knowledge of Tetrablemmidae.

The delimitation of Tetrablemmidae is quite easy when compared with many other spider families living in the ground layer of tropical forests (Oonopidae, Anapidae, Symphytognathidae, etc.). The genera *Gossiblemma* and *Diblemma* were independently removed from the vicinity of tetrablemmids by Shear (1978). I do not agree with him in synonymization of *Diblemma* with *Opopaea*, although these genera seem to be confamilial, even after the obligatory splitting of Oonopidae auct.

The relationship between Tetrablemmidae and various Haplogyne families has been discussed by Brignoli (1973, 1975, 1978c) and Shear (1978). In the recent rearrangement of main groups of spiders (Lehtinen 1978) Tetrablemmidae (listed there as Pacullidae s. lat.) was placed into Sicarioidea within the newly delimited suborder Theraphosomorpha. Thus all recent authors agree with the placement of Tetrablemmidae into the same superfamily, although it is called Scytodoidea by Brignoli (1975, 1978c).

The mutual phylogenetic relationship between families of Sicarioidea can be worked out first when the majority of recently collected material from various expeditions has been described according to modern taxonomic standards. The older descriptions of Haplogyne spiders usually included no detailed information about the inner structures of genital organs and as in case of Tetrablemmidae, only a minor part of the species and genera of these ground-living tropical groups are known.

In my opinion, the presence of the chelical lamina in Sicarioidea is an excellent instance of synapomorphy, and all Haplogyne groups that share this character are related to each other, including groups that are correctly left outside Sicarioidea, e.g., Caponiidae, Pholcidae, and the cribellate family Filistatidae (cf. also new opinions of Brignoli, 1978c).

In addition to all published information concerning Haplogyne spiders, some notes about unpublished Haplogyne material have been used in the discussion of interfamilial relationships in this paper. The most important part of this material consists of a few undescribed species of Neotropical Diguetsids,

including species with sclerotized abdomen and species with cephalic horns in males. A wide variation in vulval structures and several,

not closely related genera of Ochyroceratidae with cephalic horns in males are also worth mentioning here.

2. Methods

2.1. Laboratory methods

All drawings of carapace, abdomen, and chelicerae as well as many drawings of male palpi and other details were made with a drawing apparatus attached to a Wild M-5 or Leitz stereomicroscope. Vulval mounts were drawn from specimens cleared in lactic acid, or in the case of thick or large specimens, dissected ventral parts of abdomen treated in KOH or lactic acid. Some male palpi were also cleared with lactic acid in order to demonstrate the course of the ejaculatory duct. The mounts were drawn with a drawing apparatus attached to a Wild M-20 microscope.

The SEM micrographs were made with JEOL's JSM U-3 from specimens glued with colloidal silver and coated with Au-Pt-Ir (Au-dominated alloy for routine use in dentistry). The micrographs were all made by the author.

2.2. Terminology of tetrablemmid structures

The terminology used for abdominal sclerites and most other external details characteristic of Tetrablemmidae only has been invented by Shear (1978), and it is accepted in toto except for the following details.

The six eyes of Tetrablemmidae and all Sicarioidea consist of anterior and posterior lateral eyes and posterior median eyes. Shear regarded the anterior pair of eyes in the central position as AME, although they are ALE in an exceptional position in the compact eye pattern. All direct eyes (= AME) are absent in most families of Sicarioidea, but present in Plectreuridae.

When two separate processes are present in the distal part of the bulb, they are called embolus and conductor, independent of the homology of the latter, but basal projections of the embolus are not included in the concept of conductor. Shear included these projections in his concept of conductor. The distinction between conductor and distal modifications of the bulb remains quite artificial in males of the genus *Matta*.

Shear named all ventral abdominal scuta (pulmonary, postgenital, preanal, and anal plates), but he did not discuss the lateral or posterior plates separately. They are numbered here I—IV, the most ventral being the first. The homology of the extra plates of Pacullinae is separately discussed on p. 77. The minute plates between the anterior margins of the dorsal abdominal scutum and the pulmonary plate (sometimes fused together) are simply called anterior plates.

A completely new terminology is suggested for the sclerotized parts of the tetrablemmine vulva and some additional structures of the genital area, peculiar to this group only.

The posterior margin of the pulmonary plate is distinctly folded in all females of Tetrablemmidae. It is called the epigynal fold. The unpaired part of the vulval ducts is called the copulatory channel, independent of possible sclerotizations around it. The more or less tubular sclerotizations around the copulatory channel are collectively called the vulval stem. The paired lateral extensions of the vulval stem are called the lateral horns, but in deviating cases extensions of the vulval stem are more properly called the ventral or even anterior horns. The separate vulval plate dorsal to the copulatory channel and attached to the inner posterior margin of the pulmonary plate is called the inner vulval plate. Its trifurcate type has a central branch and two lateral branches. The sac-like unpaired vulval process attached dorsally to the anterior margin of the vulval stem is called the central process.

2.3. Taxonomic principles

The aim of this paper is to revise a quite poorly known spider family using modern taxonomic principles. For such groups, the strict application of the theoretical principles of any modern school of taxonomy is useless bickering. We need a synthesis of all information available and as phylogenetic a classification as possible.

The taxonomic terms used here do not reflect any opinions in favour of or against any schools, and the term phylogenetic in particular is only used to describe genealogical

relationships. As pointed out elsewhere (Lehtinen 1979), synapomorphy is a very useful tool of practical taxonomy and as such is also applicable outside the circle of strict supporters of the Hennigian school, but not all phyletic relationships can be described in terms of simple, externally visible synapomorphies. In practice, the creation of cladograms without shown synapomorphies for every genus separately is preferred to suggestion of synapomorphies for incompletely known similarities. The resulting classification must fit into the evolution of all possible characters, not only those selected for compilation of the cladogram. The detailed discussion of different groups shows that the evolution of Tetrablemmidae is crowded with parallelisms, discontinuous appearance of "similar" apomorphies that could easily be interpreted as synapomorphies, and repeated problems of polarity of evolution of single characters.

The criterion of monophyly includes only common origin and inclusion of all taxa with common origin (cf. Platnick 1978:368). The use of a traditional concept of similarity is included in the practical, diagnostic separation of paraphyly and polyphyly. Polyphyly is here correlated with similarity by convergence, and proven cases of polyphyletic taxa are not accepted. Paraphyletic taxa are originally based on similarities through symplesiomorphies (Hennig 1966), but in practice they are accepted by supporters of the school of evolutionary taxonomy only when they represent distinct grades as a result of essential biological improvement (Huxley 1959). Paraphyletic taxa are not intentionally accepted for Tetrablemmidae, but their presence is possible, as it is in any poorly known group.

The geographical variation of all spiders is poorly known. This is especially true for tropical areas as much of the research with modern taxonomic methods has been concentrated on the Holarctic fauna. The geographic speciation in most parts of the Holarctic region is strongly affected by its geological history, which is entirely different from that of most tropical areas.

As stated by Mayr (1963:501) "The Indo-Australian archipelago offers an ideal situation for isolation and has resulted in the produc-

tion of superspecies in almost any kind of organism that occurs there". The concept of superspecies (Mayr 1931) or geographical superspecies (Cain 1955) and its closely related components (semispecies: Mayr 1963; allo-species: Amadon 1966) has most often been applied to birds and other taxonomically well-known groups, but as stressed by Mayr (1963:500) "superspecies seem to be even more common than in birds in groups of animals with lower dispersal facilities".

Until now the evolution and speciation of Indo-Australian spiders has not been described in relation to problems of semispecies, although the concept of species by Forster & Wilton (1968, 1973), Forster (1970), and Forster & Blest (1979) conforms with these principles.

As stated above the main factor responsible for the development of superspecies is the restricted capacity for easy dispersal. Where spiders are concerned, the efficiency of dispersal is very different in different families. Geologically speaking the habitats of the Holarctic region are more unstable than many tropical habitats, and thus the efficiency of dispersal in Holarctic groups is on an average superior to many tropical groups, especially those living in the ground layer of stable tropical forests. Active movements in many Linyphiidae and Erigonidae make their aerial dispersal exceptionally efficient, while hard sclerotization of Tetrablemmidae makes their dispersal even more inefficient than that of other families living in the same habitat. Consequently, patterns of evolution and speciation between the much studied Linyphiidae-Erigonidae complex and Tetrablemmidae are entirely different. It can also be noted here that no species of Tetrablemmidae is known to be regularly anthropochorous.

The gene pool of some families of spiders is very heterogeneous, resulting in marked structural variation of many striking characters. This is obviously useful for groups living in the vegetation layer (Araneidae, Metidae, Uloboridae, Thomisidae, etc.) and therefore common in them, but seldom present in cryptic groups.

The present study is based on more than 2500 specimens of Tetrablemmidae. Several samples of single populations are represented by large numbers of both sexes and also, for-

tunately enough, often by good samples of related, allopatric taxa. This material shows that the morphological variation within all studied taxa in Tetrablemmidae is exceptionally low, usually practically absent, except for slight variation in size and shape of the dorsal abdominal scutum in females. Morphologically uniform taxa with fairly large total range are quite rare. In the case of Oriental species, *Fallablemma greeni* is the only exception, and even its known range extends only over northern and central Celebes. I have not personally analyzed the variation within the suggested, widespread, Central American *Caramatta sbordonii*, but it may represent another instance in Tetrablemmidae. The eyeless populations of *C. sbordonii* and *Ablemma shimojanai* probably belong to the same taxa as their four-eyed neighbours.

Some standards for taxonomy of any group are necessary, and they are best established when a worldwide revision of the group is made. I have chosen here, for Tetrablemmidae, standards for species and subspecies that have the maximum information value in practice. Allopatric, ecologically different populations whose morphological variation does not overlap at all are treated as different species if at least one of these species is represented by a sample in which the actual variation can be analyzed with sufficient statistical reliability. In the case of only one diagnostic character this theoretical minimum size for such a population is from 40 to 50, but in the presence of distinct gaps in several, independently variable diagnostic characters this minimum size can be correspondingly lowered. At the other end of this mathematical principle we find the normal taxonomic procedure: in the presence of a distinct morphological gap between two single specimens they are treated as different species if the gap is very large or if it is simultaneously present for a large number of characters.

If there is some overlap between the structural characters of two sufficiently large allopatric populations, these populations are treated as subspecies. The lack of positive samples from large intervening areas with similar habitats and sufficient collecting activities with standardized, effective methods is useful

additional information in the interpretation of borderline cases.

By strongly increasing the number of tetrablemmid samples from the Oriental-Australian region the patterns of evolution in this group can be more accurately mapped, and naturally the interpretation of the taxonomic status of some taxa may be altered.

The application of the above-described taxonomic principles has been used in the treatment of the following groups of allopatric taxa, each constituting a typical superspecies:

- Lamania nirmala* — *bernhardi*
Brignoliella massai — *klabati* — *maros*
B. martensi — *besuchetiana*
Ablemma lempake — *merotai* — *circumspectans*
Shearella lilawati — *selvarani*
Tetrablemma viduum — *helenensis*
T. mardionoi — *manggarai*
and, resulting in subspecific status, in:
Afroblemma thorelli thorelli — *thorelli maniema*
Ablemma (Bannia) kaindi kaindi — *kaindi avios*
Tetrablemma (T.) medioculatum medioculatum — *medioculatum gangeticum* — *medioculatum cochinese*

All other species of Tetrablemmidae are based on radical differences in a number of diagnostic characters, comparable to generally used standards for any animal group.

Subgenera and tribes are auxiliary taxonomic categories that are consistently used only when a group is well known and when the application of consistent principles has been used throughout for main taxonomic categories. In my opinion, they are useful only when a sufficient number of the dominant species of a region have been studied. Thus, e.g., the placing of the genus *Cuangoblemma* is treated with conservative principles here as the tetrablemmid fauna of most African regions is still undescribed. In many cases, it is a matter of opinion whether subgenera, tribes, and other auxiliary categories should be used or not. A sound principle always seems to be the avoidance of unnecessary names, when their use does not apparently add information about details of cladistic phylo-

geny. The three large genera, *Tetrablemma*, *Brignoliella*, and *Ablemma* could equally well have been treated in a different way, but I have chosen the classification that I hope best demonstrates the gaps actually found in their taxonomic analysis.

3. Classification

Tetrablemmidae O. Pickard-Cambridge, 1873

Tetrablemmidae O. Pickard-Cambridge, 1873. Proc. Zool. Soc. London 1873: 114.

Tetrablemmidae, Bertkau, 1878. Arch. Naturg. 44: 374 (emendation).

Phaedimoidae Thorell, 1890. Ann. Mus. Civ. Genova 28: 232 (based on homonymous type genus).

Pacullae Simon, 1893. Hist. Nat. Aragn. 1 (3): 569 (interpreted as a name of family category by ICZN 1964 § 36), Paculleae in index, p. 1079.

Pacullidae, Thorell, 1898. Ann. Mus. Civ. Genova 39: 282.

For taxonomic history of Tetrablemmidae and Pacullinae separately, see Table 2 on p. 11.

Diagnosis: Haplogyne spiders of various sizes. Colouration uniform, yellowish to dark reddish-brown. Abdomen with complicated patterns of scuta; normally includes a large dorsal scutum, four ventral scuta, and four narrow lateral and posterior scuta. Sexual dimorphism common; includes modifications in carapace, chelicerae, sternum, pattern of abdominal scuta, and sporadically modifications in first legs and gnathocoxae. Median lamina of chelicerae well developed. Usually 6 or 4 eyes, sometimes only 2, 1 or 0. Legs without spines, except in leg I of some males. Large onychium with three dentate claws.

Male palpi of simple haplogyne type, without subtegulum and seldom with conductor. Female genital orifice usually unpaired, vulva with paired soft receptacula and sclerotized plate of variable structure.

Description: Total length 0.7–9.5 mm. Carapace pear-shaped, oval or circular in female, often bearing anterior, dorsal or posterior modifications, especially in male, but also in some females. Eye pattern variable, from basic haplogyne pattern (*Segestria*) to compact.

Chelicerae with a well-developed median lamina, but, in contrast to other families of Sicarioidea, there are sometimes teeth, carina, or a notch between base of the fang and the lamina. Anterior face of chelicerae often, but not always, variably modified in males, less conspicuously also in females.

Labium basolaterally with sharp angles, short

The category of subfamily must be absolutely comparable to the treatment of all families, at least within the same order. With these premises, there is only one choice: the acceptance of two well-defined subfamilies in Tetrablemmidae.

trapezoidal to rounded triangular. Gnathocoxae distally pointed and with parallel median margins as in all Sicarioidea. Sternum wide, posteriorly truncate or concave, or with posterior pit or rugose process.

Typical pattern of abdominal scuta consists of a dorsal scutum extending over the whole dorsum, a large ventral pulmonary plate, including orifices of petiolus and anterior spiracula, a narrow postgenital plate, a wider preanal plate, and an anal plate surrounding the spinnerets. Usually four lateral plates, the most ventral of which are variably reduced in many species.

Six spinnerets of unmodified general type as is widespread in Sicarioidea. Colulus a small knob with a few hairs, sometimes totally reduced.

Anterior pair of respiratory organs long and fairly narrow in species studied so far; classified as book lungs in large species, but strongly reduced in most minute species and there classified as simple or reduced tracheae.

Male genital pore in the pulmonary plate or concealed behind it. Female genital orifice with the same alternative positions, but within a single group, opposite to the position of the male orifice.

Legs without normal spines, but leg I of male may have specialized spines or exceptional hair pattern, or its metatarsi or tibiae may be modified. Patellae lighter in colour than the other leg segments. Tarsi and femora without trichobothria, all metatarsi with a single trichobothrium in position 0.35–0.75. Tibiae with two dorsal rows of trichobothria, usually mainly in subbasal to subcentral position and an additional long central trichobothrium, usually slightly distal to the most distal trichobothria of the two rows. Tarsal organ large, in position 0.4–0.7.

Three tarsal claws in well developed onychium, paired claws pectinate in single row. Female palpus usually slightly reduced in size, distally with translucent, straight claw.

Surface of carapace and sternum variably rugose, reticulate or pitted; abdominal scuta with hairs, variable in surface structure.

Ultrastructure of skin, hairs, and sensory organs variable, also within related groups (Figs. 1 a–g & 2 a–j). Surface of legs coarsely transversely furrowed as in Palpimanidae or convergently in

some families of Araneomorpha (Anapidae, Textri-cellidae) or almost smooth as in Diguettidae (Lehtinen, unpublished). Ultrastructure of the trichobothrial basal plate without distinct transverse or longitudinal furrows, but sometimes with a few concentric folds as in Diguettidae, Palpimanidae, Segestriidae, and some Pholcidae (Lehtinen, unpublished). Wide variation of this plate between main groups of Tetrablemmidae as is typical of Sicarioidea. Tarsal organ long, oval and with large depression (Fig. 1 g) and therefore not recognized as a tarsal organ by Shear (1978: 6, fig. 3). Normal and modified hairs representing several different types that can be derived from the serrate type of *Segestria* (see Lehtinen 1975 a & b, figs 5–6). There is always a longitudinal furrowed structure of the hairs, which gives rise to the secondary hairs. Thus fundamentally different from the plumose type of hairs typical of all Amaurobiomorpha (see Lehtinen 1967: fig. 8). Slit sense organs as in most groups of spiders.

Male palpus with unmodified or slightly modified femur, patella, and tibia. Cymbium usually strongly reduced in size or with two lobes, but normal in two genera. Bulbus pear-shaped to globular, usually terminal, subtegulum absent as in all Sicarioidea. Embolus variable in structure, but often terminal and fairly simple. Conductor present in several distantly related lineages.

Female external genitalia include different modifications of the pulmonary plate, either an unpaired, marginally sclerotized pit or paired depressions. Vulval structure variable, but seminal receptacula always soft, at least the receptacula proper. A sclerotized plate attached to the inner posterior margin of the pulmonary plate always present, but its shape is quite variable.

Web known in detail for only one species, *Brignoliella vulgaris*. It is a small dense sheet attached along the surface of large dry leaves. Judging from centrally placed, circular, woven plates in some of the webs inhabited by female specimens the cocoons may be attached to the web.

Female and male tetrablemmids are most probably always efficiently locked together during copulation although no direct observations of copulation have been made.

Two different locking mechanisms have been found by the author through analysis of the functional morphology of sex-linked characters. The most widespread locking mechanism consists of cheliceral tooth of male fitting into pits (or central unpaired pit) in the preanal plate of female. This locking mechanism is widespread in Ablemini and Brignoliellini, and probably present in some Tetrablemmi. The other locking mechanism is found mainly in the large genus *Ablemma*, but in a less striking form also at least in *Anansia*. This mechanism consists of a central acute process or spine on the male carapace fitting into a pit in female sternum. In less striking cases, the posterior face of the sternum is simply widely concave, and the corresponding male process is less acute.

The inner vulval plate of some Pacullinae include steering knobs for embolus and attached structures.

The functional significance of the conductor is not yet known.

All species of Tetrablemmidae live in litter or moss in tropical or subtropical forests. A few species have further adapted to life in caves, under bark of trees, and one species (*Shearella lilawati*) is known to live mainly in dry, sandy, coastal habitats.

Pacullinae Simon, 1893

For a complete list of synonyms, see Table 2. However, this list is partly misleading, because most of the authors using the name Pacullinae have in fact been dealing with representatives of Tetrablemmidae only (Simon 1893, Roewer 1942, Brignoli 1972 a and later). They have based the definition and limitation solely on species belonging to Tetrablemmidae, but have referred to a name of a taxon that has the type genus based on real paculline species.

Simon (1893) first used a group name Paculleae above the generic level, but he placed this group in Theridiidae. Thorell (1898) established Pacullidae as a family name, but Brignoli (1973) first used the subfamily name Pacullinae as a subordinate group of Tetrablemmidae.

Diagnostic characters of Pacullinae have been compared with those of Tetrablemmidae in Table 1. Paculline species are most easily separated from all tetrablemmine species by much larger size, heavily rugose carapace and sternum, entirely different patterns of sexual dimorphism, as well as different patterns of abdominal scuta. Paculline species are separated from Neotropical, sclerotized species of Diguettidae by presence of complex pattern of abdominal scuta.

Shear's (1978) description of Pacullidae is based on a few species of *Paculla* and *Lamanina* only. As such it can be used only for definition and limitation of this group of genera, and only when crucial information about the horns of thoracic area in the type-species of both genera is added.

Pacullinae has plesiomorphic eye pattern, male cymbium, female copulatory pit, and seminal receptacula. Besides this, its sexual dimorphism is slight throughout, in comparison with that of Tetrablemmidae.

Sclerotization patterns of carapace and

Table 1. Subfamilies of Tetrablemmidae

	Pacullinae	Tetrablemminae
Size	3—9.5 mm	0.7—2 mm
Sexual dimorphism in male		
— eye region	unmodified	usually modified
— clypeus	unmodified or marginal tooth	high, often with horns or other modifications
— anterior face of chelicerae	unmodified	usually with tooth or boss
— metatarsi and tibiae I	both with spines or cusps if modified	usually unmodified, rarely with tooth but no spines
— postgenital plate	strongly reduced or absent	slightly larger or subequal
— lateral abdominal plates	plate I totally reduced	similar to those of female
— genital pore	in pulmonary plate (behind pulmonary plate in female)	behind pulmonary plate (behind or in pulmonary plate in female)
Eye pattern	three pairs	three pairs or compact
— number of eyes	six	6, 4, 2, 1, or 0
Cheliceral teeth	1—2 or rugose carina in ♂♀	none in ♀, notch in some ♂
Shape of labium	rounded triangular	short trapezoidal
Surface of chitinous plates		
— carapace	roughly pitted	reticulate or granulated, seldom partly pitted
— sternum	roughly pitted	reticulate or pitted
— pulmonary plate	centrally roughly pitted	reticulate or totally pitted
— dorsal abdominal scutum	centrally uneven, marginally smooth	smooth or slightly pitted, seldom reticulate
Sternal modifications (when present)	posterior sternal apophysis in both sexes	sternal pit or posterior concavity in females, posterior modifications in a few species
Abdominal scuta		
— dorsal abdominal scutum	sometimes reduced in size, shape long oval	subcircular to long oval
— postgenital plate	wide, laterally tapering in females	usually narrow and with parallel margins
— preanal plate	1 large central + 2 small lateral or entire, sometimes reduced to minute plates	entire, often with copulatory grooves or pits
— lateral plates	usually 4 in females, 3 in males, each row variably bordered with rows of small plates	4 or seldom 3 in both sexes, first plate variably reduced
— posterior plates	4—8 rows of small plates	4 continuous plates entire, female plate posteriorly folded
— pulmonary plate	sometimes with separate stigmal plates	
Position of trichobothrium on mt I	0.5—0.75	0.33—0.46
Pattern of tibial trichobothria	2 rows + unpaired central in basal 2/3	2 rows + unpaired central in basal half
Leg indexes		
— tibial index	0.7—1.15	0.37—0.63
— f+pat+tib+mt+t/carapace (1)	2.92—3.97	1.78—2.64
Male palpal characters		
— cymbium	normal or short, two-lobed	very short, distally obtused
— position of bulbus	ventral or subventral	terminal or subterminal
— shape of bulbus	subglobular or U-shaped	subglobular to pyriform
— type of embolus	thick, distally lobed or laminar	usually thin, distally pointed, sometimes modified
— conductor	lacking	sometimes present
— course of ejaculatory duct	simple, more or less uncoiled	usually with basal and/or distal loops
— basal segments of palpus	unmodified	often slightly modified

Female genital characters

— copulatory orifice	large, paired or unpaired, posterior to pulmonary plate	usually minute unpaired, sometimes large, anteriorly moved
— epigynal fold	lacking	always present, sometimes with modifications
— vulval ducts	soft, short	soft, variable in length
— seminal receptacula	always soft	sometimes partly sclerotized
— inner vulval plate	? only one large vulval plate, homology uncertain	always separate from other sclerotized parts, trifurcate, seldom simple
— central vulval process	lacking	usually present, sac-like, sometimes reduced or modified
— sclerotizations around the copulatory channel	only one plate (see above)	vulval stem and lateral, ventral or anterior projections
Web structure	unknown	dense sheet web
Cocoon	carried by chelicerae	fixed in centre of the web
Distribution	Oriental	Pantropical

Table 2. Placing of Pacullidae and Tetrablemminae (references in brackets = technical change without study of tetrablemmid material).

Pacullinae	Tetrablemminae
	Tetrablemmidae: O. Pickard-Cambridge, 1873 (des); (Bertkau, 1878); Crosby, 1934; Gertsch, 1941, 1977; Marples, 1955, 1964; Brignoli, 1975, 1976, 1978a, b; Benoit, 1977; Blandin, 1977; Shimojana 1977
Dysderoidea: Thorell, 1881	Dysderidae: Simon, 1889
Phaedimoidae: Thorell, 1890	
(Theridiidae: Pacullae: Simon, 1893)	Theridiidae: Pacullae: Simon, 1893
Pacullidae: Thorell, 1898	
Theridiidae: Paculleae: Hogg, 1920	Theridiidae: Simon, 1905; Berland, 1920; Simon & Fage, 1922
(Theridiidae: Pacullinae: Petrunkevitch, 1928; Bonnet, 1945—61)	(Oonopidae: Petrunkevitch, 1928; Bonnet 1945—61)
(Theridiidae: Pacullinae: Kaston, 1938)	Oonopidae: Gamasomorphinae: Butler, 1932
(Theridiidae: Pacullinae: Roewer, 1942)	(Oonopidae: Gamasomorphinae: Kaston, 1938)
	Oonopidae: Tetrablemminae: Bryant, 1940; Komatsu, 1968
	(Oonopidae: Gamasomorphinae & Theridiidae: Pacullinae: Roewer, 1942)
Tetrablemmidae: Levi & Levi, 1962	Tetrablemmidae: Levi & Levi, 1962
	Hadrotarsidae: Roewer 1963a, b
(Pacullidae: Brignoli, 1972a, b)	Oonopidae: Levi, 1968
(Tetrablemmidae: Pacullinae: Brignoli, 1973)	Pacullidae & Tetrablemmidae: Brignoli, 1972a, b
	Tetrablemmidae: Tetrablemminae & Pacullinae: Brignoli, 1973, 1974
	Caponiidae: Tikader, 1975
Pacullidae: Lehtinen, 1978	Pacullidae: Lehtinen, 1978
Pacullidae: Shear, 1978; Deeelman-Reinhold, 1980	Tetrablemmidae: Tetrablemminae & Brignoliellinae: Shear, 1978, 1979; Bourne, 1980; Deeelman-Reinhold, 1980

Table 3. Measurements of Tetrablemmidae

	carapace	abdomen	leg I	leg & carapace indexes
Pacullinae				
<i>Mirania armata</i>	♂ 2.25 1.52 1.00	2.15 1.71	2.33 0.67 1.94 1.42 0.90	0.86 3.22 0.63 1.48
<i>Paculla sulaimani</i>	♂ 1.49 1.01 0.63	1.71 1.26	1.56 0.44 1.56 1.18 0.70	1.05 3.65 0.60 1.48
<i>P. negara</i>	♀ 1.90 1.47 0.85	2.79 1.72	2.32 0.59 2.16 1.62 0.85	1.14 3.97 0.52 1.29
<i>Lamania nirmala</i>	♂ 2.44 1.70 1.01	-	2.55 0.75 2.28 1.84 0.93	0.93 3.42 0.51 1.44
	♀ 2.42 1.70 1.05	3.45 2.32	2.73 0.73 2.43 1.96 1.00	0.88 3.66 0.50 1.42
<i>L. bernhardi</i>	♀ 2.38 1.64 0.97	3.15 2.16	2.46 0.71 2.20 1.82 0.95	0.96 3.43 0.50 1.45
<i>Sabahya kinabaluana</i>	♂ 1.54 1.18 0.59	1.98 1.41	1.45 0.48 1.10 0.84 0.63	0.72 2.92 0.75 1.31
	♀ 1.62 1.28 0.59	2.34 1.54	1.54 0.44 1.24 0.99 0.65	0.77 3.00 0.66 1.27
<i>"Paculla" cameronensis</i>	♂ 2.00 1.52 0.73	2.63 1.72	1.88 0.61 1.64 1.38 0.85	0.82 3.18 0.62 1.32
Tetrablemminae				
<i>Afroblemma t. thorelli</i>	♂ 0.46 0.36 0.24	0.59 0.42	0.33 0.12 0.19 0.14 0.18	0.42 2.09 1.29 1.28
	♀ 0.45 0.36 0.22	0.66 0.43	0.32 0.12 0.19 0.13 0.18	0.43 2.09 1.38 1.25
<i>Fallablemma greenei</i>	♂ 0.54 0.47 0.33	0.77 0.60	0.45 0.15 0.30 0.20 0.21	0.56 2.43 1.05 1.15
	♀ 0.57 0.47 0.33	0.87 0.67	0.41 0.15 0.24 0.19 0.22	0.42 2.12 1.16 1.21
<i>Indicoblemma sheari</i>	♂ 0.47 0.38 0.23	0.62 0.47	0.32 0.12 0.24 0.17 0.19	0.51 2.21 1.12 1.23
	♀ 0.49 0.36 0.25	0.63 0.50	0.30 0.12 0.22 0.17 0.18	0.44 2.02 1.06 1.36
<i>Chavia monticola</i>	♂ 0.59 0.46 0.29	0.97 0.72	0.40 0.15 0.29 0.21 0.24	0.49 2.19 1.14 1.28
<i>Singaporemma halongensis</i>	♂ 0.41 0.36 0.27	0.60 0.44	0.31 0.13 0.21 0.16 0.16	0.51 2.37 1.00 1.14
	♀ 0.44 0.36 0.29	0.62 0.45	0.27 0.13 0.18 0.15 0.15	0.41 2.00 1.00 1.22
<i>S. adjacens</i>	♂ 0.44 0.37 0.26	0.58 0.52	0.27 0.13 0.23 0.16 0.16	0.52 2.16 1.00 1.19
	♀ 0.46 0.38 0.29	0.67 0.55	0.30 0.13 0.22 0.14 0.15	0.48 2.04 1.07 1.21
<i>Pahanga lilisari</i>	♂ 0.65 0.57 0.42	0.87 0.70	0.50 0.18 0.37 0.26 0.26	0.55 2.42 1.00 1.14
	♀ 0.64 0.54 0.40	0.88 0.73	0.52 0.18 0.37 0.24 0.26	0.56 2.45 1.08 1.19
<i>P. diyaluma</i>	♂ 0.59 0.50 0.39	0.91 0.71	0.44 0.16 0.30 0.19 0.23	0.51 2.24 1.21 1.18
<i>P. centenialis</i>	♀ 0.54 0.44 0.30	0.70 0.56	0.37 0.14 0.27 0.19 0.19	0.50 2.15 0.97 1.23
<i>Borneomma (B.) roberti</i>	♂ 0.63 0.55 0.48	0.91 0.69	0.52 0.13 0.35 0.24 0.24	0.56 2.35 1.00 1.15
<i>B. (Oleoblemma) yuata</i>	♂ 0.51 0.48 0.35	0.64 0.55	0.41 0.14 0.26 0.18 0.18	0.51 2.29 1.02 1.06
	♀ 0.52 0.44 0.33	0.76 0.61	0.33 0.14 0.24 0.18 0.18	0.46 2.06 1.00 1.18
<i>Brignolliella (B.) acuminata</i>	♂ 0.57 0.48 0.30	0.74 0.61	0.42 0.15 0.30 0.20 0.20	0.53 2.23 1.00 1.19
	♀ 0.57 0.46 0.32	0.88 0.64	0.39 0.14 0.29 0.22 0.23	0.51 2.23 1.05 1.24
<i>B. (B.) vitiensis</i>	♂ 0.58 0.46 0.34	0.76 0.63	0.40 0.14 0.27 0.19 0.21	0.47 2.05 1.11 1.26
<i>B. (B.) trifida</i>	♂ 0.50 0.42 0.30	0.64 0.50	0.34 0.14 0.24 0.18 0.19	0.48 2.18 1.06 1.19
<i>B. (B.) carmen</i>	♂ 0.69 0.56 0.34	0.88 0.69	0.53 0.17 0.36 0.25 0.26	0.52 2.28 1.04 1.23
	♀ 0.67 0.54 0.38	0.99 0.79	0.46 0.17 0.34 0.24 0.24	0.51 2.16 1.00 1.24
<i>B. (B.) bicornis</i>	♀ 0.65 0.54 0.38	0.96 0.79	0.48 0.16 0.34 0.26 0.27	0.52 2.32 1.04 1.20
<i>B. (B.) martensi</i>	♂ 0.77 0.64 0.38	1.05 0.79	0.61 0.22 0.48 0.30 0.33	0.61 2.52 1.10 1.20
	♀ 0.80 0.67 0.43	1.12 0.79	0.62 0.22 0.48 0.32 0.34	0.54 2.38 1.04 1.27
<i>B. (B.) vulgaris</i>	♂ 0.53 0.46 0.35	0.71 0.61	0.41 0.14 0.27 0.20 0.21	0.51 2.32 1.05 1.15
	♀ 0.58 0.48 0.34	0.77 0.67	0.40 0.14 0.26 0.20 0.21	0.45 2.09 1.08 1.21
<i>B. (B.) maros</i>	♂ 0.53 0.44 0.31	0.71 0.61	0.38 0.14 0.26 0.18 0.19	0.49 2.17 1.06 1.20
	♀ 0.57 0.46 0.28	0.85 0.65	0.40 0.15 0.25 0.18 0.19	0.44 2.05 1.06 1.24
<i>B. (B.) klabati</i>	♂ 0.54 0.49 0.31	0.86 0.67	0.40 0.14 0.29 0.22 0.22	0.54 2.35 1.02 1.10
<i>B. (B.) massai</i>	♂ 0.52 0.49 0.36	0.74 0.62	0.41 0.14 0.28 0.20 0.20	0.54 2.37 1.00 1.06
	♀ 0.56 0.48 0.35	0.79 0.73	0.41 0.14 0.28 0.20 0.21	0.50 2.21 1.08 1.14
<i>B. (Ceratoblemma) michaeli</i>	♂ 0.62 0.53 0.45	0.71 0.61	0.45 0.15 0.34 0.23 0.24	0.55 2.27 1.04 1.17
	♀ 0.59 0.52 0.38	0.86 0.73	0.44 0.13 0.32 0.23 0.23	0.54 2.29 1.00 1.13
<i>"Brignolliella" sarawak</i>	♂ 0.61 0.53 0.37	0.85 0.73	0.38 0.16 0.29 0.25 0.25	0.48 2.18 1.00 1.15
<i>Ablemma (A.) baso</i>	♂ 0.41 0.33 0.32	-	0.29 0.11 0.19 0.12 0.16	0.47 2.12 1.33 1.24
	♀ 0.42 0.30 0.25	0.53 0.37	0.27 0.11 0.17 0.13 0.16	0.41 2.00 1.23 1.40
<i>A. (A.) sternofoveata</i>	♀ 0.37 0.30 0.23	0.50 0.44	0.26 0.10 0.18 0.12 0.14	0.49 2.16 1.17 1.23
<i>A. (A.) berryi</i>	♂ 0.42 0.35 0.28	0.48 0.40	0.35 0.12 0.20 0.14 0.15	0.48 2.29 1.07 1.20
<i>A. (Bannia) k. kalndi</i>	♂ 0.56 0.48 0.38	0.70 0.55	0.44 0.14 0.32 0.20 0.21	0.57 2.34 1.05 1.17
	♀ 0.59 0.48 0.36	0.82 0.64	0.42 0.15 0.30 0.21 0.22	0.51 2.20 1.04 1.23
<i>A. (B.) k. avios</i>	♂ 0.60 0.46 0.39	0.76 0.61	0.50 0.15 0.38 0.21 0.22	0.63 2.43 1.05 1.30
	♀ 0.62 0.50 0.32	0.88 0.69	0.46 0.14 0.34 0.21 0.23	0.54 2.23 1.10 1.24
<i>A. (B.) circumspectans</i>	♂ 0.54 0.44 0.40	0.72 0.51	0.42 0.15 0.34 0.19 0.21	0.63 2.43 1.11 1.23
	♀ 0.55 0.44 0.33	0.70 0.56	0.41 0.14 0.30 0.18 0.21	0.56 2.25 1.16 1.25
<i>A. (B.) merotal</i>	♂ 0.49 0.42 0.36	0.57 0.51	0.34 0.14 0.26 0.17 0.19	0.53 2.24 1.12 1.17
<i>A. (B.) lempake</i>	♂ 0.43 0.37 0.34	0.54 0.44	0.31 0.13 0.22 0.14 0.15	0.51 2.21 1.04 1.16
	♀ 0.50 0.34 0.21	0.54 0.50	0.29 0.13 0.19 0.14 0.14	0.38 1.78 1.03 1.47
<i>A. (B.) samarinda</i>	♂ 0.44 0.38 0.29	0.61 0.48	0.33 0.14 0.24 0.14 0.17	0.55 2.32 1.34 1.16
<i>A. (B.) sedgwicki</i>	♂ 0.38 0.33 0.28	0.50 0.39	0.27 0.11 0.19 0.13 0.14	0.50 2.21 1.08 1.15
<i>A. (B.) singalang</i>	♂ 0.47 0.40 0.33	0.54 0.46	0.34 0.13 0.25 0.16 0.17	0.53 2.23 1.06 1.18
<i>A. (B.) datahu</i>	♂ 0.44 0.39 0.23	0.55 0.45	0.32 0.13 0.26 0.15 0.16	0.59 2.32 1.07 1.13
	♀ 0.48 0.38 0.20	0.60 0.48	0.33 0.13 0.22 0.16 0.16	0.46 2.08 1.00 1.26
<i>A. (B.) rososae</i>	♂ 0.42 0.35 0.27	0.52 0.40	0.27 0.13 0.22 0.15 0.16	0.52 2.21 1.07 1.20
<i>A. (B.) erna</i>	♂ 0.48 0.40 0.41	0.58 0.52	0.40 0.13 0.28 0.17 0.18	0.58 2.42 1.06 1.20
	♀ 0.51 0.39 0.32	0.65 0.60	0.37 0.13 0.25 0.17 0.18	0.49 2.16 1.06 1.31
<i>A. (B.) girinum</i>	♂ 0.38 0.31 0.29	0.50 0.38	0.26 0.10 0.22 0.14 0.16	0.58 2.32 1.14 1.23
<i>A. (B.) pugnax</i>	♀ 0.46 0.34 0.26	0.66 0.44	0.31 0.10 0.22 0.14 0.17	0.48 2.04 1.21 1.35
<i>A. (B.) syahdani</i>	♀ 0.48 0.37 0.30	0.65 0.50	0.34 0.13 0.23 0.16 0.16	0.48 2.17 1.00 1.30
<i>A. (B.) ruohomaekii</i>	♂ 0.48 0.40 0.34	0.67 0.45	0.36 0.11 0.29 0.17 0.17	0.60 2.29 1.00 1.20
	♀ 0.50 0.37 0.29	0.71 0.48	0.36 0.11 0.25 0.17 0.17	0.50 2.12 1.00 1.35
<i>A. (B.) makiling</i>	♂ 0.50 0.42 0.35	0.67 0.46	0.34 0.14 0.27 0.18 0.19	0.54 2.24 1.06 1.19
	♀ 0.52 0.41 0.24	0.61 0.52	0.34 0.14 0.26 0.17 0.18	0.50 2.10 1.06 1.29
<i>Sulaimania vigelandi</i>	♂ 0.33 0.26 0.18	0.36 0.29	0.22 0.08 0.13 0.10 0.10	0.39 1.91 1.00 1.30

	carapace	abdomen	leg I	leg & carapace indexes
<i>Hariblemma pandani</i>	♂ 0.48 0.39 0.24	0.69 0.53	0.36 0.13 0.25 0.17 0.22	0.52 2.35 1.29 1.23
	♀ 0.49 0.40 0.27	0.72 0.58	0.36 0.13 0.25 0.18 0.22	0.51 2.38 1.22 1.23
<i>Shearella lilawati</i>	♂ 0.55 0.48 0.33	0.90 0.74	0.49 0.13 0.34 0.25 0.24	0.63 2.64 0.96 1.15
	♀ 0.58 0.50 0.28	0.97 0.84	0.50 0.13 0.34 0.25 0.24	0.59 2.52 0.96 1.16
<i>S. selvarani</i>	♂ 0.52 0.43 0.34	0.82 0.66	0.40 0.11 0.29 0.23 0.23	0.56 2.42 1.00 1.21
	♀ 0.54 0.45 0.28	0.99 0.92	0.37 0.11 0.30 0.23 0.23	0.55 2.30 1.00 1.20
<i>S. browni</i>	♂ 0.53 0.44 0.26	0.82 0.59	0.41 0.15 0.30 0.23 0.24	0.57 2.51 1.04 1.20
<i>Gunasekara ramboda</i>	♂ 0.69 0.63 0.53	1.03 0.86	0.55 0.18 0.34 0.28 0.30	0.49 2.39 1.07 1.10
	♀ 0.64 0.53 0.38	0.99 0.90	0.48 0.16 0.33 0.25 0.28	0.51 2.34 1.12 1.21
<i>Singalangia sternalis</i>	♂ 0.47 0.41 0.22	0.74 0.52	0.36 0.13 0.23 0.19 0.20	0.48 2.36 1.05 1.15
<i>Tetrablemma (Kumaonia) loebli</i>	♂ 0.45 0.35 0.19	0.55 0.44	0.26 0.13 0.19 0.14 0.15	0.43 1.93 1.07 1.27
	♀ 0.48 0.38 0.25	0.64 0.51	0.30 0.13 0.21 0.12 0.16	0.44 1.92 1.33 1.25
<i>T. (Indonops) deccanensis</i>	♂ 0.50 0.40 0.27	0.70 0.53	0.36 0.13 0.27 0.19 0.19	0.53 2.28 1.00 1.25
	♀ 0.50 0.39 0.27	0.78 0.56	0.34 0.12 0.25 0.19 0.19	0.50 2.19 1.00 1.28
<i>T. (I.) samoensis</i>	♂ 0.53 0.44 0.30	0.93 0.63	0.32 0.13 0.27 0.21 0.23	0.50 2.19 1.10 1.20
	♀ 0.51 0.42 0.30	0.82 0.61	0.32 0.13 0.23 0.17 0.21	0.44 2.08 1.24 1.21
<i>T. (I.) helenensis</i>	♂ 0.51 0.40 0.24	0.77 0.56	0.37 0.13 0.24 0.20 0.18	0.46 2.16 0.92 1.30
<i>T. (I.) benoitii</i>	♀ 0.44 0.32 0.21	0.51 0.46	0.35 0.11 0.18 0.14 0.16	0.41 2.14 1.14 1.38
<i>T. (I.) marawula</i>	♂ 0.41 0.37 0.28	0.59 0.49	0.32 0.10 0.20 0.15 0.17	0.49 2.29 1.12 1.11
	♀ 0.46 0.37 0.23	0.68 0.53	0.33 0.10 0.21 0.16 0.17	0.46 2.11 1.06 1.24
<i>T. (I.) mardionoi</i>	♂ 0.42 0.37 0.31	0.54 0.46	0.28 0.12 0.19 0.14 0.15	0.45 2.10 1.07 1.14
	♀ 0.45 0.38 0.23	0.62 0.52	0.31 0.12 0.19 0.14 0.16	0.43 2.04 1.14 1.18
<i>T. (I.) manggarai</i>	♂ 0.46 0.38 0.30	0.55 0.49	0.32 0.11 0.21 0.15 0.16	0.46 2.07 1.03 1.21
	♀ 0.48 0.40 0.26	0.72 0.57	0.33 0.11 0.23 0.16 0.16	0.48 2.06 1.00 1.20
<i>T. (I.) vietnamensis</i>	♂ 0.49 0.42 0.24	0.81 0.63	0.40 0.14 0.28 0.21 0.20	0.57 2.51 0.95 1.17
<i>T. (I.) phulchoki</i>	♀ 0.49 0.38 0.25	0.65 0.51	0.30 0.13 0.22 0.17 0.20	0.45 2.06 1.18 1.28
<i>T. (T.) m. medioculatum</i>	♂ 0.51 0.40 0.34	0.68 0.57	0.36 0.13 0.27 0.16 0.15	0.53 2.10 0.94 1.28
<i>T. (T.) m. gangeticum</i>	♂ 0.50 0.42 0.30	0.70 0.59	0.32 0.12 0.25 0.17 0.17	0.50 2.06 1.00 1.18
	♀ 0.46 0.41 0.25	0.76 0.63	0.31 0.12 0.22 0.17 0.17	0.48 2.15 1.00 1.12
<i>T. (T.) m. cochinese</i>	♂ 0.48 0.42 0.28	0.69 0.58	0.34 0.13 0.25 0.16 0.17	0.50 2.19 1.03 1.12
	♀ 0.48 0.41 0.24	0.70 0.59	0.29 0.12 0.23 0.17 0.17	0.48 2.04 1.00 1.19
<i>T. (T.) rhinoceros</i>	♂ 0.48 0.39 0.33	0.65 0.54	0.35 0.12 0.22 0.17 0.16	0.46 2.13 0.94 1.23
	♀ 0.49 0.40 0.27	0.67 0.67	0.33 0.12 0.20 0.17 0.17	0.41 2.02 1.00 1.23
<i>T. (T.) brignolii</i>	♂ 0.50 0.42 0.29	0.69 0.56	0.33 0.14 0.24 0.16 0.16	0.48 2.06 1.00 1.18
	♀ 0.50 0.42 0.23	0.82 0.65	0.31 0.13 0.23 0.17 0.17	0.46 2.06 1.12 1.18
<i>T. (T.) okei</i>	♂ 0.51 0.42 0.29	0.78 0.57	0.40 0.12 0.25 0.19 0.19	0.49 2.25 1.00 1.21
	♀ 0.50 0.40 0.26	0.78 0.61	0.33 0.14 0.23 0.18 0.18	0.46 2.12 1.00 1.25
<i>Cuangoblemma machadoi</i>	♂ 0.38 0.29 0.21	0.48 0.34	0.25 0.10 0.16 0.11 0.12	0.43 1.95 1.09 1.31</

sternum, modifications of the lateral, ventral, and dorsal abdominal scuta, distal structures of embolus, as well as complex structure of the inner vulval plate represent distinctly apomorphic states. Thus it is obvious that Pacullinae and Tetrablemminae cannot be derived from each other, but are results of divergent evolution of common ancestors; more exactly a group that does not exist any more, but that has sometimes been a sister group of past Diguettidae. For details of discussion concerning the phylogenetic relationships of Pacullinae, see p. 78.

The relative number of striking apomorphies is larger in Tetrablemminae, and because of that Pacullinae is treated first.

Species of Pacullinae are known only from a restricted part of the Oriental region, from the base of the Malayan Peninsula (southern Burma) to the western corner of New Guinea. None of the known species are either frequent or abundant, and very few adult specimens of the whole subfamily are known. All the specimens collected by the author come from shaded forest habitats: either from moist leaf litter or ground layer moss in mountain forests. No webs were observed, but they are most probably webspinners, as at least some Tetrablemminae and all Diguettidae.

In this study, Pacullinae is divided into two tribes, Peraniini and Pacullini. This has not been done for the clarity of the classification of the subfamily Pacullinae itself, but rather as a treatment consistent with Tetrablemminae. In the latter subfamily, the use of tribes as an auxiliary category is very useful for a quick survey of the phylogeny.

Peraniini, tribus n.

Largest tetrablemmid spiders (4.3–9.5 mm). Pattern of abdominal scuta strongly reduced. No cheliceral teeth, but a chitinous keel or irregular rugosity present between the base of fang and the cheliceral lamina.

Male palpal cymbium normal in contrast to all other groups of Tetrablemmidae, bulbus large, U-shaped.

Female pulmonary plate with paired depression.

First leg of male with ventral spicules.

Distribution from Sumatra to southern Burma.

Perania Thorell, 1890

Perania, Thorell, 1890. Ann. Mus. Civ. Genova 28: 315.

Phaedima, Thorell, 1890. Ann. Mus. Civ. Genova 28: 305, not *Phaedima* Thorell, 1881.

Perania, Simon, 1893. Hist. Nat. Araign. 1 (3): 572.

Paculla, Simon, 1893. Hist. Nat. Araign. 1 (3): 572. (in part).

Perania, Hogg, 1920. J. Fed. Malay st. Mus. 8: 81, figs. 1 a, b, d, f and (carapace only) 1 & 1 c, not 1 c (= *Leucauge* sp.)

Perania, Levi & Levi, 1962. Bull. Mus. Comp. Zool. 127: 64, fig. 307.

Phaedima, Levi & Levi, 1962. Bull. Mus. Comp. Zool. 127: 64, fig. 308.

Paculla, Shear, 1978. Amer. Mus. Novit. 2650: 41 (in part, *Perania korinchica* Hogg, 1920 erroneously included in *Paculla*).

Perania, Shear, 1978. Amer. Mus. Novit. 2650: 41.

Type-species by original designation and monotypy *Perania pallida* Thorell, 1890 from Sumatra = *Perania nigra* (Thorell, 1890). In this study, *P. nigra* is selected as the valid of two simultaneously published, synonymic names. *P. nigra* is based on adult material of both sexes, *P. pallida* on a juvenile specimen from the same locality.

Large (6.5–9 mm), elongate paculline spiders with strong reduction of lateral, postgenital, preanal, and dorsal abdominal plates. Carapace relatively longer than in other genera of Pacullinae, cephalic area raised, clypeus high. Eyes on shallow tubercles only, situated far from the front margin of rounded carapace. Male clypeus with small acute tooth at the lower margin.

Dorsal abdominal scutum small, central, unevenly undulating in surface structure. Metatarsi I of males with short spicules.

Male palpal cymbium long, unmodified, bulbus U-shaped, embolus thick, distally laminar.

Type of epigynal orifices and vulval structure unknown, but paired vulval sclerotizations shining through the integument far from the posterior margin of the pulmonary plate.

Distribution Sumatra and southern Burma.

Separated from *Mirania* by larger size, lack of long teeth in the thoracic area, as well as presence of clypeal modifications in male. Further separated from the single known species of *Mirania* by strongly reduced pattern of abdominal plates, although this may not be an important generic character.

Related to *Mirania* because of synapomorphy of all male palpal characters. Type of female genital organs very different from that of *Pacullini*, although inner details are not known.

Representatives of this genus, including the largest known tetrablemmids, have not been collected for one hundred years, except the single carapace of a female specimen, described by Hogg (1920) and also seen by Shear (1978) and myself. The adult specimens of *Perania*, originally described under *Phaedima* by Thorell (1890) were never studied for taxonomy of Tetrablemmidae, but they have

been continuously catalogued under *Paculla* since Simon (1893 b). On the other hand, the juvenile type specimen of the type-species of *Perania* has been generally regarded as an enigmatic species (cf. Shear 1978: 41). Levi & Levi (1962) studied the paculline material of the Genoa museum for their revisional study of Theridiidae, but only to exclude them from that family. However, they first suggested that the type-specimen of *Perania pallida* could be a juvenile tetrablemmid. Unfortunately, Levi & Levi (1962) further confused the information about these poorly known paculline species through unintentional mixing up of the data of Sumatran and New Guinean species.

During this study, but unfortunately long before collection of my own paculline material, I have had the opportunity to superficially study the existing type material of Thorell's Pacullinae. It was not possible to make accurate drawings with the aid of microscopical drawing equipment but freehand sketches and detailed notes were made.

The type locality of two valid species of *Perania* (also the type locality of *Mirania armata* and that of the juvenile type of *Perania pallida*) is the volcanic mountain Singalang in western Sumatra. This mountain was therefore recently visited by me. Although I analysed all altitude zones and all different types of habitat in them, only a single male specimen of *Mirania armata* was found. There are many reasons to believe that the largest tetrablemmid species are now rarer than a hundred years ago. Firstly, the total number of spiders collected from the Singalang area by me was much greater than the material published by Thorell (1890). Secondly, I am rather well acquainted with the typical habitats of all groups of Tetrablemmidae, and collected four new species of minute Tetrablemminae (*Pahanga lilisari*, *Ablemma singalang*, *Tetrablemma mardionoi*, and *Singalangia sternalis*) in the type locality of *Perania nigra* and *P. picea*, and a fifth (*Ablemma erna*) in large quantities elsewhere in the Sumatran mountains without collecting a single juvenile of Pacullinae.

Perania pallida was originally included in a new genus by Thorell (1890) because he did not know the juvenile characters of Pacullinae.

The identification of the type-species has to be based on the relative size of the type specimen which seems to be two molts from the adult stage. The intensity and sequence of the sclerotization of juvenile pacullinae is certainly similar in all genera, and sufficient juvenile specimens of *Paculla*, *Lamania*, *Sabahya*, and some unnamed species have been available for me to identify the stage of this type-specimen. Adult specimens of *P. picea* are much larger than those of *P. nigra*, while the presence of thoracic teeth as small elevations should be visible in juveniles of *M. armata* as they are actually present in juveniles of that stage in *Lamania nirmala*. Additional material from the common type locality could hardly throw more light on this problem of identity of the type specimen of *P. pallida*, and the aim of this detailed discussion is to stabilize the suggested solution.

Perania nigra (Thorell, 1890), comb. n.
Figs. 6, 8 & 9.

Phaedima nigra, Thorell, 1890. Ann. Mus. Civ. Genova 28: 310 (♂♀).

Perania pallida, Thorell, 1890. Ann. Mus. Civ. Genova 28: 316 (juv.), n. synonym.

Paculla nigra, Simon, 1893. Hist. Nat. Araign. 1 (3): 572.

Phaedima granulosa, Levi & Levi, 1962. Bull. Mus. Comp. Zool. 127: 64, fig. 308, not *P. granulosa* Thorell, 1881.

Lectotype ♂ and allotype ♀, both designated here, from Sumatra (Indonesia, Sumatera Barat), Mt. Singalang, O. Beccari 1878, in MCSN (Genoa), examined; juvenile holotype of *Perania pallida* with the same data, in MCSN (Genoa), examined.

Male 6.5 mm, female 7 mm. Carapace completely granulated, male with a short, acute tooth in the clypeal margin. Sternum densely pitted, posteriorly drawn to a rounded knob. Dorsal abdominal scutum much smaller than the dorsum, centrally with divergent coarse ridges and undulations. Pulmonary and anal plates well developed, but rest of abdomen covered with minute plates in longitudinal rows corresponding to lateral and posterior scuta, post-genital and preanal plates, and marginal parts of dorsal abdominal scutum.

Spiracula far behind petiolus, in male close to the margin of pulmonary plate, but in female in small separate marginal plates.

Metatarsi I of male with 4 prolateral short spicules, corresponding to modified bases of hairs. Distal part of anterior metatarsi densely covered with hairs in both sexes.

Male bulbus U-shaped, embolus shorter than in *P. picea*.

Female pulmonary plate with superficial paired depression strongly anterior to the margin. Paired vulval structure shining through this area.

Separated from *P. picea* by smaller size and by details of genital organs, and from sympatric *Mirania armata* by larger size and absence of thoracic teeth.

The freehand sketch published by Levi & Levi (1962: fig. 308) undoubtedly represents a species of *Perania* and not *Phaedima granulosa*. As these authors refer to study of type material in the Genoa museum, it is evident that there was a later confusion in labelling of the sketches. This opinion is further supported by the discussion in Levi & Levi (1962: 64): "It is likely that *Perania pallida* is a juvenile female of *Phaedima granulosa* Thorell. Both come from Sumatra." According to different embolus lengths I have listed their drawing under *P. nigra* and not *P. picea*, although the distal part of the embolus in that figure does not conform to either of these species.

Perania picea (Thorell, 1890), comb. n.
Figs. 7 & 11.

Phaedima picea, Thorell, 1890. Ann. Mus. Civ. Genova 28: 305.

Paculla picea, Simon, 1893. Hist. Nat. Araign. 1 (3): 572.

Perania korinchica, Hogg, 1920. J. Fed. Malay St. Mus. 8: 81, figs. 1 a, b, d, f and figs. 1 & 1 e in part (carapace only), not fig. 1 c, n. syn.

Lectotype ♂ and allotype ♀, both designated here, from Sumatra (Indonesia, Sumatera Barat), Mt. Singalang, O. Beccari 1878, in MCSN (Genoa), examined; holotype ♀ of *Perania korinchica* Hogg, 1920 from Sumatra, Korinchi peak (= Indonesia, Sumatera Barat, Gunung Kerintji), Sungei Kumbang (1450 m), H. C. Robinson & C. Boden Kloss 1914, in BMNH (London), examined.

Male 9 mm, female 9.5 mm. Carapace in both sexes as in *P. nigra*, but larger. Dorsal abdominal scutum almost smooth, with only minor undulations. Reduction of abdominal plates as in *P. nigra*. Sexual dimorphism in the area of spiracula as in *P. nigra*. Male palpal bulbus U-shaped, but embolus both absolutely and relatively much longer.

Paired depressions in the "epigynal area" of the pulmonary plate distinctly narrower than in *P. nigra*.

Hogg (1920) included his *P. korinchica* in the correct genus with the wrong argumentation: "Dr. Thorell founded the genus *Perania* for a species of which the abdomen was wholly soft, while in *Paculla* they have a hard

shield protecting that portion of the body. The single female in this collection which I now describe has the soft abdomen and therefore comes into the latter genus". The type vial of *P. korinchica* still contains the small abdomen of *Leucauge* sp., and it is difficult to believe that any arachnologist could connect that with the large, rugose carapace of the largest known species of Tetrablemmidae. The synonymization of *P. korinchica* is based only on the similar size, but it is highly improbable that the western Sumatran mountains could have yet a third species of *Perania*, identical in carapace structure and size to *P. picea*.

Perania birmanica (Thorell, 1898), comb. n.

Paculla birmanica (Thorell, 1898). Ann. Mus. Civ. Genova 39: 282.

Holotype ♀ from Burma, vicinity of Bia-pó, Mt. Carin Chebà, originally in MCSN (Genoa), not found in 1975.

This large species (7.5 mm) is the only paculline species that has not been studied by either myself or Shear (1978). Thorell (1898) compared this species with *Mirania armata*, and all details of his description fit my concept of *Perania*, but not other genera of Pacullinae. *P. nigra* is as large as *P. birmanica* and thus the synonymy of these species cannot be totally excluded, but the same species of this group most probably cannot be found in both Sumatra and in Burma. Besides this, *P. birmanica* was not originally compared with *P. nigra*, although Thorell described the latter simultaneously with *armata*. There is also a possibility that *P. birmanica* is a large, toothless relative of *M. armata*, as closely related pairs of paculline spiders with and without thoracic teeth are known in *Lamania* and possibly congeneric pairs of such species are also known in *Paculla*.

Mirania, gen. n.

Type-species *Phaedima armata* Thorell, 1890 from Sumatra.

Medium-sized (4.3–5 mm), dark brown, strongly rugose spiders with long paired teeth in the thoracic area. Male clypeus unmodified, metatarsi of leg I modified as in *Perania*. Abdominal plates slightly reduced, when compared with *Paculla*, *Lamania*, and *Sabahya*, but postgenital and preanal plates easily recognizable. Lateral plates posteriorly branched, posterior rows of small plates therefore numerous.

Male bulbus U-shaped as in *Perania*.

Female genital characters not described by Thorell (1890), no female specimens preserved in museums.

Mirania armata (Thorell, 1890), comb. n.
Figs. 3–5, 10 & 12, Table 3.

Phaedima armata Thorell, 1890. Ann. Mus. Civ. Genova 28: 313. (♀).

Paculla armata, Simon, 1894. Hist. Nat. Araign. 1 (3): 373.

Two ♀ syntypes from Sumatra (Indonesia, Sumatera Barat), Mt. Singalang and Lubu Selassi, O. Beccari 1878, originally in MCSN (Genoa), destroyed by flooding (empty broken vials with type labels examined). A male from type locality, the base of Mt. Singalang, is now selected as neotype, because there are no difficulties in identification of this species — even though the original material belongs to the opposite sex. Collecting data for the neotype ♂: Indonesia, Sumatera Barat, Padangpanjang district, Lembah Anai, 4 km SW of Padangpanjang, moist jungle slope with leaf litter (900 m), 26.IX. 1978, PTL, in MZT (Turku).

Male 4.3 mm. Shape of carapace and eye pattern as in *Perania* spp., but clypeal horn absent. Thoracic area with long, paired, distally pointed processes directed slightly backwards. Whole carapace rugose because of granules, bearing long hairs. These granules are mainly in sparse longitudinal rows in the strongly elevated cephalic area, but in marginal parts of the thoracic area in rows radiating from the central smooth area around shallow fovea. Clypeus very high, convex, without true granules, but with faint transverse furrows and long hairs obliquely directed towards the median line.

Chelicerae anteriorly slightly concave, transversely faintly furrowed, but without modifications or granules other than the median carina typical of all Pacullinae. Cheliceral fang short, basally thick, rapidly tapering. Base of fang without well-defined teeth, but with some rugosity. Structure of labium and gnathocoxae as in other Pacullinae, distal rounded half of labium distinctly separated from the trapezoidal basal half by a transverse furrow.

Sternum relatively longer than in *Paculla* and related genera, completely covered with rounded granules, median line with narrow smooth area in anterior half. Posterior end of sternum with rugose, slightly elevated area — a sternal apophysis characteristic of all other known species of Pacullinae is not present. Shear (1978) used distinct sternal apophysis as a family character for his Pacullidae.

Abdomen with a thick scutum dorsally, extending ca. 3/4 of the length of dorsum. Margins of scutum strongly bent upwards. Surface of central area consists of irregularly spaced cones, surrounded by radiating furrows, resembling a miniature landscape with mountains and valleys. The surface is completely covered with fine hairs.

Pulmonary and anal plates well developed as in all species of Pacullinae. Postgenital plate represented by only three transverse rows of small plates, each

of them much larger than the usual minute plates with one hair which occur in all tetrablemmids. The total width of these plates is almost the width of the anal plate. A deep wavy furrow between the second and third rows of these plates is completely sclerotized to the bottom. Pulmonary plate anteriorly sparsely covered with hairs, originating posterior to small crescent-shaped elevations. Posterior part of pulmonary plate strongly rugose because of irregular transverse furrows. Large crescent-shaped spiracula close to the posterior margin of pulmonary plate, and large circular genital pore is ca. two diameters from the posterior margin of the pulmonary plate.

Lateral scuta all broken into rows of small plates. There are five distinctly separated rows of plates in anterior half of abdomen, but these are posteriorly branched to form seven regular rows between dorsal scutum and anal plate.

Metatarsi I with seven irregularly spaced spicules ventrally, distal hair covering of metatarsi less dense than in *Perania* spp. All legs are more robust than the legs of *Paculla* and related groups.

The male palpus is close to that of *Perania picea*. The lamellar apex of embolus is weakly sclerotized.

Female 5 mm. The original description of Thorell (1890) is fairly long, and it is obvious that there is no marked sexual dimorphism, except the more distinct postgenital plate. The thoracic teeth are also present in female, and most probably as well developed as in male.

Separated from other species of Pacullinae by the pattern of abdominal scuta that is intermediate between the normal pattern in Pacullini, and the strongly reduced pattern in *Perania*. Differentiated from other species with long thoracic spines by U-shaped cymbium.

Pacullini, tribus n.

Medium-sized (3.2–5.3 mm) tetrablemmid spiders. Three lateral scuta in males, four in females. Preanal plates well developed in both sexes, postgenital plate quite narrow in males, wide and laterally tapering in females. Chelicerae with one or two distinct teeth between the base of fang and the cheliceral lamina.

Male palpal cymbium bilobate, bulbus subglobular.

Female pulmonary plate without distinct depressions. Female genital orifice paired or unpaired, inner vulval plate tubular, variably sclerotized. Receptacula entirely soft-walled.

First leg of male unmodified or with short spines or patterns of special hairs.

Distribution from Malaya to western New Guinea.

Paculla Simon, 1887

Phaedima, Thorell, 1881. Ann. Mus. Civ. Genova 17: 232. Junior homonym of *Phaedima* Robineau-Desvoidy, 1863.

Paculla, Simon, 1887. Ann. Soc. Ent. France, Ser. 6: 7, Bull., CXCV as a *nomen novum* for *Phaedima* Thorell, 1881; not *Paculla*, Simon, 1893 & 1894.

Paculla, Shear, 1978. Amer. Mus. Novit. 2650: 41, in part.

Type-species of *Phaedima* Thorell, 1881: *P. granulosa* Thorell, 1881 from New Guinea.

Medium-sized (3.2–5 mm) dark brown, strongly rugose spiders. Paired thoracic horns quite short or absent. Legs relatively longer than in other genera of Pacullinae, especially in males. Pattern of abdominal scuta not reduced, males with 3 lateral scuta, with or without parallel rows of small plates, females with 4 lateral scuta.

Male palpal cymbium distally obtuse, with two lobes. Bulbus subglobular, embolus terminal, without basal modifications. Apex of embolus branched or at least modified, one branch with thin lamellar wings.

Female copulatory opening paired, its halves separated by a well-sclerotized septum. Inner epigynal plate without lateral constrictions, but with central pockets.

The presence or absence of spines on metatarsi and tibiae of male legs I as well as the type of embolus are mentioned here with some reservation, because the monophyly of all the species listed here in *Paculla* is not indisputable. The congenerity of the only known female with the male of the type-species is not confirmed, although it is quite probable.

The distribution of named species of *Paculla*, as this genus is delimited here, extends from Malayan Peninsula to western New Guinea.

Paculla granulosa (Thorell, 1881)
Figs. 14 a & b.

Phaedima granulosa, Thorell, 1881. Ann. Mus. Civ. Genova 17: 233 (♂).

Paculla granulosa, Simon, 1887. Ann. Soc. Ent. France, Ser. 6, Bull., CXCIX.

Holotype ♂ from Dutch New Guinea (Indonesia, Irian Barat), Ramoi, O. Beccari, in MCSN (Genoa), examined.

Male 5 mm. Detailed description by Thorell (1881). This species is separated from all other known species of *Paculla* by larger size and by presence of short, paired horn in the thoracic area of carapace. It is further separated from *P. sulaimani* (with similar type of male palpus) by presence of rows of minute plates above lateral abdominal plates II–IV, and from *P. negara* by different modifications of the embolus apex.

Paculla sulaimani, sp. n.
Figs. 13–15, Table 3.

Holotype ♂ from Malaysia, Selangor, Kuala Lumpur, Lembah Pantai, in jungle litter close to the university, 12.XI.1976, PTL, in MZT (Turku).

Male 3.2 mm. Carapace low, sparsely granulated over whole surface, but surface between the granules smooth. No traces of horns in thoracic area. Chelicerae anteriorly straight, but median margin with a very distinct carina, and a transversal thin ridge basally parallel to the clypeal margin. Base of fang with an indistinct, blunt tooth at the upper margin of the cheliceral lamina.

Sternum completely covered with hairs in pits. Margins of these hair pits with four radiating ridges as in *Sabaha kinabaluana*. Dorsal abdominal scutum convex, sparsely covered with hairs in small, simple pits, intervening areas smooth. Margin of dorsal abdominal scutum hairless, but otherwise this plate is more similar to the dorsal abdominal scutum of Tetramminae, including the yellow-brown colour.

Pulmonary plate smooth, except for sparsely spaced hairs in pits. These hair pits are simple in posterior part of the pulmonary plate, but anteriorly swollen in the anterior parts. Hairs around the protruding genital pore and sublateral stigmata shorter than the remaining hairs.

Postgenital plate quite narrow, entire, but centrally constricted. Two small extra plates behind the posterolateral corners of the pulmonary plate. Preanal plate rounded quadrangular, extending close to the postgenital plate. A pair of fairly large triangular plates at the anterolateral corners of the preanal plate with projecting, dark, obtuse corners, obviously homologous with the separate plates of other *Paculla* and *Lamania* spp.

Lateral abdominal plates I–III fairly wide, covered all over with several rows of hairs, but not flanked by rows of minute plates as in all other known species of *Pacullini*. Anterior ends of these lateral scuta unequal, II much shorter than I & III. Lateral margin of dorsal abdominal scutum flanked by a row of small plates (as lateral scuta of other species of *Paculla*). Posterior scuta represented by four rows of small plates, being continuations of lateral plates I–III and the above-mentioned row of small plates.

Legs yellowish-brown, slender, all segments without spines, cusps, or other modifications.

Male palpal cymbium obtusely bilobate, palpal tibia long, centrally swollen. Bulbus subglobular, embolus long, slightly curved. Apex of embolus bilobate, distance between these lobes small, margins of the outer lobe thinly membranous. Course of the ejaculatory duct not totally visible, but the anterior half of the bulbus is filled with a large, oval part, abruptly narrowing close to the base of embolus, and thereafter transversely coiled before entering the embolus.

P. sulaimani is separated from all known species of *Paculla* and related genera by the pattern and surface structure of the abdominal scuta. However, its palpus is close to that of the type-species of *Paculla*, and separated from that only by closer position of the lobes of the embolic apex and absence of wide, distal membranous lamina of embolus.

Female unknown.

Paculla negara Shear, 1978
Figs. 17, 20, 22. Table 3.

Paculla negara Shear, 1978. Amer. Mus. Novit. 2650: 44, fig. 123 (♂).

Holotype ♂ from Malaysia, Terengganu, Taman Negara, hill near Kampong, 26.IV.1973, D. H. Kistner & H. E. Jacobsen, in MCZ (Cambridge), examined.

Suggested allotype ♀ from Malaysia, Selangor, Templer Park, Hutan Simpang, jungle litter, 20.XI.1979, PTL, in MZT (Turku). 1 juv. specimen from Templer Park, 4 km SE of Hutan Simpang, most probably belongs to this species.

Male 3.48 mm, described in detail by Shear (1978). Chelicerae with 2 distinct teeth between the base of fang and margin of cheliceral lamina. Metatarsi and tibiae I–II with small, irregular spines (macrosetae of Shear 1978). Postgenital scutum centrally separated into two short plates. Cymbium without distinct mesial lobe, but cymbial hairs relatively longer than in other species of *Paculla*. Embolus distally entire, but flanked on both sides with a thin membrane.

Female 3.9 mm. Carapace low, thoracic area without traces of paired horns. Colouration dark brown, surface sparsely granulated, intervening areas finely reticulate. Eyes subequal in size, PME separated by slightly less than one diameter from each other and one diameter from ALE. ALE and PLE on very distinct tubercles. Anterior cheliceral face as in *P. sulaimani*. One strong tooth between the base of fang and the cheliceral lamina.

Sternum completely very rugose due to almost continuous outer, swollen margins of the hair pits. These pit margins are simply crescent-shaped and thus different from corresponding modifications in *P. sulaimani*. Posterior sternal apophysis well developed as in all *Paculla* spp.

Dorsal abdominal scutum long oval, its posterior margin almost transverse. Marginal area hairless but with strongly wrinkled surface. Central part sparsely covered with thin hairs, surface smooth, but uneven through large, irregularly transversal, slightly elevated areas. Pulmonary plate with long hairs in anterior half, short hairs with minute pits along the posterior margin. Anterior hairs with strongly swollen pits as in sternum.

Postgenital plate wide, tapering towards both ends, quite similar to postgenital plates of females of *Lamania* spp. Preanal plate and bordering smaller plates as in *Lamania* spp. The pulmonary plate is strongly convex, and the preanal plate is obliquely directed over posterior margin of pulmonary plate. Thus the preanal plate in Fig. 17 is shown much shorter than its real shape in horizontal position. Three minute plates between postgenital and preanal plate (as in all *Lamania* spp.) mostly concealed behind the postgenital plate. Four narrow lateral plates, each of them ventrally flanked by a row of minute plates. These rows of small plates are absent in anterior part, being shortest (less than 1/2) in plate I and longest in plate IV. There is a double

row of minute plates along the margin of the dorsal abdominal scutum. Anterior ends of the lateral plates quite unequal. Plate IV is continuous, but the anterior margin is lighter and conspicuous due to a few long hairs on this part. Plate I extends further than III and II (shortest), and anterior ends of both sides of plate I are connected with a row of coarse hairs. Posterior scuta represented by the continuous and one centrally deficient row of small plates. These plates are quite small and circular in marginal parts of these rows, but incompletely fused together to constitute larger plates in central parts of the three upper rows.

Female copulatory opening paired large and separated from each other by a dark, chitinous extension of the inner vulval plate. Inner vulval plate large, anteriorly semicircular, marginally convex and dorsally furnished with distinct folded pockets. Strongly sclerotized lateral margins continued by thin transversely furrowed membrane along the inner face of the pulmonary plate. Posterior corners of this membranous plate with separate, sclerotized, convex plates (not shown in Fig. 22).

The conspecificity of the above female with the holotype ♂ is not finally confirmed. According to size, this female can only be conspecific with *P. negara* as far as known species of western Malaysia are concerned. The pattern of abdominal scuta is not contradictory to that of *P. negara* male, taking into account the patterns of sexual dimorphism in the related genus *Lamania*. There is a single cheliceral tooth between the base of fang and the cheliceral lamina in this female, but two teeth in the male holotype. Intraspecific variation of this unique pattern of cheliceral armature (only in Pacullinae, but not in all species, e.g., the practically sympatric *P. sulaimani*) is not known. The rugosity of carapace, sternum, and pulmonary plate is as heavy as in the male holotype as studied by me, but unfortunately no notes were made about the exact shape of the swollen margins of the hair pits — a character that finally excludes the conspecificity of this female with *P. sulaimani*. As the male of "*P. cameronensis*" is distinctly larger than this female specimen, the latter can only represent the female of *P. negara* or that of an undescribed species.

This is the only known female of the genus *Paculla* as delimited here, but only the finding of the female of *P. granulosa* can finally solve the problem of delimitation of *Paculla*.

The male *P. negara* is separated from all known males of *Paculla* by spine pattern of legs as well as structure of the embolic apex.

Lamania, gen. n.

Paculla, Shear, 1978. Amer. Mus. Novit. 2650: 41, in part.

Paculla, Deeleman-Reinhold, 1980. Zool. Meded. 56: 57, in part.

Paculla, Brignoli, 1981. Bull. Soc. Ent. Ital. 113: 5. Type-species *L. nirmala* n. sp. from Borneo.

Medium-sized (3–5.5 mm), dark brown, strongly rugose spiders. Paired thoracic horn long or absent. Other non-genital characters diagnostic for the whole genus largely as in *Paculla*.

Male palpal bulb distally obtuse, embolus marginal or submarginal. Embolus shorter and relatively much thicker than in *Paculla* spp. Apex of embolus with complex lobes.

Female copulatory orifice large as in *Paculla*, but unpaired, elongate oval, without any traces of central septum. Inner vulval plate large, without pockets.

Known distribution Malayan Peninsula, Borneo, and Celebes.

Lamania nirmala sp. n.

Fig. 21. Table 3.

Holotype ♂, alloparatype ♀, and 1 ♀ 2 juv. paratypes from Indonesia, Kalimantan Timur, Bulungan district, Tarakan Island, Yuata, in litter of wet palm jungle, 1.XI.1979. PTL, in MZT (Turku).

Tarakan Island, Simpangan Sasani, in jungle litter, 1.XI.1979, PTL: 1 juv.

Male ca. 4.5 mm (abdomen absent in holotype). Carapace low, surface smooth or very finely reticulate, except regular rows of elevated hairs pits, arranged radially from the foveal area. Shape of swollen outer margins of the hair pits acutely triangular. Thoracic area with a pair of long, distally acute spines as in *Mirania armata*. PME and PLE subequal in size, ALE distinctly smaller, lateral eyes on very distinct elevations. PME separated by less than half of their diameter from each other and ca. one diameter from ALE.

Anterior face of chelicerae as in *Paculla* spp. A blunt, basally wide tooth or boss between the base of fang and the cheliceral lamina.

Legs slender, no modifications in leg I.

Male palpal tibia strongly swollen. Cymbium distally blunt, weakly bilobate, laterally not modified. Bulbus shorter than wide. Ejaculatory duct not visible. Embolus short and thick, basal part with a dorsal obtuse process. Apex of embolus with two lobes, inner lobe pointed, outer lobe distally hammer-shaped and with inner, membranous wing.

Female 5.3 mm. Carapace, eyes, chelicerae, sternum and legs as in male.

Shape of dorsal abdominal scutum as in *Paculla negara*, but marginal, bald area almost smooth. Central area smooth and with thin, sparsely spaced, long hairs. Two slightly lower, longitudinal fields along the whole length of the scutum. Anterior part of the pulmonary plate with strongly swollen, but transverse (not triangular) margins of hair pits, posterior part almost smooth, hairless, except for a crescent-shaped row of rugose hair pits, abruptly

continuing parallel to the lateral margins, but on the inner side of the stigmata. Postgenital plate wider than in *P. negara*, its anterior margin almost straight, but swollen, posterior margin smoothly curved, convex. Preanal plate wider than long, with rounded corners, posterior corners with partly separate extra plates corresponding to the totally separate plates of *L. kraui*. A row of numerous small plates between postgenital and preanal plates, four central plates concealed behind the postgenital plates. One pair of large, triangular perigenital plates.

Four lateral plates, completely flanked by ventral rows of minute plates, I & IV anteriorly continuous. Anterior end of plate II shorter than that of plate III. Double row of minute plates along the dorsal abdominal scutum as in *P. negara*. Four rows of small circular plates corresponding to lateral plates II–IV, posterior end of plate III being bifurcate. Rows of small plates posterior to lateral scutum I end at the anterior margin of the anal plate.

Copulatory orifice long, oval. Inner vulval plate with convex margins laterally and deep constrictions close to the posterior margin. Strongly sclerotized margin of the plate continued with membranous part along the inner surface of the pulmonary plate.

Separated from *L. bernhardi* only by minor details of embolus, while possible minor differences of females have not been found. In fact, all figures of the female of *L. bernhardi* in this paper were originally made of a specimen that was thought to belong to *L. nirmala*. Thus *L. nirmala* and *L. bernhardi* are allopatric closely related taxa belonging to the same superspecies. The most distinct difference between the emboli of these species is the lack of the ventral tooth at the margin of the thick embolic trunk in *L. nirmala*, but also the shape of membranous distal parts of the embolus seems to be slightly different between these two species. Separated from *L. inornata* by more complicated distal processes of embolus.

Separated from *L. kraui* by presence of paired teeth in the thoracic area and by minor differences in the genital organs of both sexes. Separated from *L. sheari* (and an undescribed species from Sabah) by unmodified leg I of male.

Lamania bernhardi (Deeleman-Reinhold, 1980), comb. n.

Figs. 18, 19 & 23.

Paculla bernhardi, Deeleman-Reinhold 1980. Zool. Meded. 56: 68, figs. 1–6.

Holotype ♂ and 2 paratypes (♀) from Sepaku, 40 km NE of Balikpapan, Kalimantan (Borneo), in litter of mixed tropical forest, 14/15.VII.1979, leg. P. R. Deeleman, in RMNH (Leiden), not examined.

Own material: Indonesia, Kalimantan Timur, Kutai district, Lao Janan, in jungle litter, 30.X.1979, PTL: 1♀. This specimen, externally identical with females of *L. nirmala* (except minor differences in colouration) was dissected and regarded as a female of *L. nirmala*, but Lao Janan is close to Sepaku (both between Samarinda and Balikpapan) and ca. 500 km from Tarakan.

Both sexes described in detail by Deeleman-Reinhold (1980). For differential diagnosis, see *L. nirmala*.

Lamania inornata (Deeleman-Reinhold) 1980), comb. n.

Paculla inornata Deeleman-Reinhold, 1980. Zool. Meded. 56: 71, figs. 7–9.

Holotype ♂ and 1 ♂ 1 ♀ paratypes from Tuaran, Sabah (Malaysian Borneo) ca. 500 m, by sieving leaf-litter in *Hevea* plantation surrounded by secondary forest. 1.VII.1979, leg. P. R. Deeleman and C. L. Deeleman, in RMNH (Leiden: 1 ♂ 1 ♀), not examined.

Male 3.46 mm, female 3.84 mm, both sexes described in detail by Deeleman-Reinhold (1980).

Separated from *L. nirmala* and *L. bernhardi* by absence of thoracic spines and by apical part of embolic modifications. Separated from *L. kraui* by absence of modified spines in the anterior part of pulmonary plate and by details of genital organs.

The original description mentions carrying of egg sack in the female chelicerae. This is the first note of Paculline behaviour referring to cocoon.

Lamania kraui (Shear, 1987), comb. n.

Paculla kraui, Shear, 1978. Amer. Mus. Novit. 2650: 41, figs. 112–120.

Holotype ♀ and alloparatype ♂ from Malaysia, Pahang, Tamerloh district, Krau Reserve, 30.VI.1973, J. Fleagle, in MCZ (Cambridge), examined.

Male 3.17 mm, female 4.1 mm. Both sexes described in detail by Shear (1978). Lateral scuta ventrally flanked by rows of minute plates in female only. Hairs of all abdominal scuta exceptionally long.

Separated from *L. nirmala* and *L. bernhardi* by lack of long teeth in the thoracic area as well as minor details mentioned above. *L. kraui* is surprisingly close to *L. nirmala* in non-genital and genital characters. The male bulbus is more elongate, but the structure of embolus is almost identical. I studied the structure of the vulva from the female holotype, dissected by Shear, and confirmed that there is no central septum in the epigynal orifice. However, the basal constrictions of the inner vulval plate are less significant in *L. kraui*.

Separated from *L. inornata* and all known species of *Paculla* by presence of basally thick setae on the anterior margin of the respiratory areas in anterior half of the ventral abdominal plate.

Although the monophyly of known *Paculla* spp. is somewhat uncertain, none of them is closely related to these four species of *Lamania*.

Lamania sheari (Brignoli, 1981), comb. n.

Paculla sheari Brignoli, 1981. Boll. Soc. Ent. Ital. 113: 5, figs. 1–3.

Holotype male from Indonesia, Sulawesi Selatan, surroundings of Rantepao, Londa, 24.I.1979, in coll. P. Brignoli, not examined.

Male 4.87 mm, carapace 2.12×2.00, leg I 2.25+0.75+1.85+1.30+0.90 mm, without thoracic spines on carapace. Described in detail by Brignoli (1981). The shape of bulbus and especially the short laminar embolic division prove that this species is a relative of all these species that have been described under *Lamania* in this paper, and it must be definitively transferred from *Paculla*. The strongly modified tibia I is unique among known Pacullinae, but this type of modification of male leg I is present also in an undescribed species from Sabah, Borneo (Deeleman-Reinhold, pers. comm.). There is also a possibility that all species with strongly modified tibia I constitute a supraspecific taxon of their own, within or close to *Lamania*. The information concerning this species was kindly sent to me by Prof. Brignoli, when the manuscript was otherwise completed and his paper was still in press.

As my specimen of Pacullinae from northern Celebes (cf. p. 24) is subadult and the non-genital characters of *L. sheari* are not known in detail for me, nothing can be said about the possible relationship or even conspecificity of these two records from Celebes. As many species are known from Borneo and at least one in New Guinea, it is probable that there are several species also in Celebes.

Sabahya Deeleman-Reinhold, 1980

Type-species *Sabahya kinabaluana* Deeleman-Reinhold, 1980 from Borneo.

Drafts of Deeleman-Reinhold's (1980) paper were seen, when this paper had been completed and accepted for printing. However, to avoid unnecessary synonyms, the names of genera and species of Deeleman-Reinhold were changed for all new species and genera from the Kinabalu region, although the

description is totally based on own material from practically the same locality.

Medium-sized (3.5–4.0 mm), dark brown spiders with short paired horn in thoracic area. Legs relatively shorter than in *Paculla* and *Lamania*. Metatarsi and tibiae of male leg I with groups of short spines. Male palpal tibia mesially modified. Embolic division complex, including several basal modifications. Tip of embolus thin, simple.

Epigynal orifices small, paired, far from each other. Inner vulval plate with paired steering knobs and lateral, spirally coiled modifications.

Distribution Borneo and probably Bali.

Sabahya kinabaluana Deeleman-Reinhold, 1980
Figs. 1 a–g, 24–30. Table 3.

Sabahya kinabaluana, Deeleman-Reinhold, 1980.
Zool. Meded. 56: 72, figs. 10–13.

Holotype ♂ and ♀♀ paratypes from National Park Kinabalu, Sabah (Malaysian Borneo). Head Quarters at 1550 m, in litter of mixed tropical rainforest 26/30.VI.1979, leg. P. R. Deeleman and C. L. Deeleman, in RMNH (Leiden), not examined. For additional topotypical material, see Deeleman-Reinhold (1980).

Own material: Malaysia, Sabah, Tuaran district, Mt Kinabalu National Park between Power Station and Layang Layang (2300 m), in moss and litter of cloud forest, 7.XI.1976, PTL: 1 ♂ 4 ♀ 5 juv. — Mt. Kinabalu N.P., Silau Silau trail (1500 m), in litter of rain forest, 10.XI.1976, PTL: 1 ♂ 1 juv., all in MZT (Turku).

Male 3.5 mm, female 4.0 mm. Male carapace with strong paired teeth, female carapace with small teeth in the same position. Surface of carapace generally smooth between the granules, but two large sublateral fields reticulated. The whole carapace sparsely covered with long hairs in semicircular pits, laterally raised to conspicuous granules. Corresponding hair pits in sternum very conspicuous, each with starlike chitinous ridges.

Dorsal abdominal scutum slightly convex, undulate but in surface structure smooth, sparsely pitted and hairy. Its margins are slightly raised and ventrally bordered by a dense row of elongate small chitinous plates. Posterior part of two upper lateral scuta also bordered with similar plates.

Lateral scutum IV of male totally absent as in all *Pacullini*, but a separate posterodorsal scutum IV is present immediately behind the dorsal scutum.

Female with lateral scuta I & IV anteriorly continuous through a row of small plates. Lateral scutum III originating parallel to them, but II first originates in front of the cover of book lungs. All lateral scuta posteriorly reach the caudal margin of the pulmonary plate, and are continued by rows of small plates. These plates of row I reach to the margin of the anal plate, while rows II & III are continued by entire posterior scuta I & IV. Lateral scutum III is continued by two parallel rows of small plates, continued later as entire posterior scuta II & III.

Postgenital plate very small in male, but in female relatively larger than in any other species of the whole family. Both postgenital and preanal plates are bordered in each sex by two lateral plates, which are distinctly larger than the numerous perigenital plates around them.

Separated from *S. bispinosa* by smaller size and different shape of carapace. Separated from all other *Pacullini* species by entirely different type of genital organs.

Sabahya bispinosa Deeleman-Reinhold, 1980

Sabahya bispinosa Deeleman-Reinhold, 1980. Zool. Meded. 56: 74, figs. 14–15.

Holotype ♀ from National Park Kinabalu, Sabah (Malaysian Borneo), Head Quarters at 1550 m, by sieving leaf-litter on side of road, 27.VI. 1979, leg. P. R. Deeleman and C. L. Deeleman, in RMNH (Leiden), not examined.

Female 4.7 mm, carapace 2.16×1.68 mm, described in detail by Deeleman-Reinhold (1980). Male unknown.

Vulva of this species was not figured, and it remains somewhat uncertain, whether this species with longer thoracic spines and strongly arched cephalic area really is congeneric with the sympatric *S. kinabaluana*. Similar structure of postgenital and preanal plates speaks in favour of such placing.

Pacullini incertae sedis

"*Paculla*" *cameronensis* Shear, 1978
Figs. 31 a & b. Table 3.

Paculla cameronensis, Shear, 1978. Amer. Mus. Novit. 2650: 43, figs. 121–122.

Holotype ♂ from Malaysia, Pahang, Cameron Highlands, VII.1948. N. L. H. Krauss, in AMNH (New York), examined.

Male 4.17 mm. Described by Shear (1978).

Shape of carapace resembling that of *P. negara*, no traces of thoracic teeth. Lateral eyes on distinct tubercles. ALE larger than PLE. PME circular, equal to ALE in size and separated from them by slightly less than their diameter; PME separated from each other by one third of their diameter.

Carapace sparsely covered with distinct granules, constituting of semicircularly raised bases of hairs. Clypeus with long hairs directed centrally, base of these hairs slightly granulate.

Chelicerae with short fang and normal lamella, three well defined conical teeth in compact group between them.

Sternal apophysis well developed. Sternal surface strongly granulate especially in distal half, a circular smooth area anterior to the centrum. Sternal granules more or less trifurcate and therefore intermediate between starlike (*Sabahya*) and simple arched (*Lamania*).

Dorsal scutum distinctly convex, in minor details fairly smooth, but three longitudinal rows of long

ridges present as in *Perania*, two lateral rows with obliquely placed ridges. Pulmonary plate with large smooth, long oval pulmonary covers. Anterior stigmatae situated half way between posterior margins of petiolus and pulmonary plate. Central field between petiolus and strongly protruding genital orifice granulate as sternum.

Two narrow postgenital plates almost fused centrally, two large perigenital plates triangular. Preanal plate twice wider than long, entire, its posterolateral corners not separated by seam as in studied specimens of *Lamania* and *Paculla*. Three fairly wide lateral plates (I, III, II), posterior half of them irregularly flanked by a few narrow, ventral plates. Row of small plates along the dorsal scutum continuous and followed by an entire, wide posterior scutum. Two additional posterior scuta formed by continuations of small plates, originating from the posteroventral corner of lateral scutum II. Additional rows of small plates between lateral and posterior scuta originating from posterodorsal corners of lateral scuta I & II as well as from posteroventral corner of lateral scutum I. Narrow chitinous ridges present between dorsal, posterior, and anal scuta. Colulus obtusely triangular, with a few hairs.

Tibia I with a ventral row of short spines flanked by rows of short thick hairs prolaterally. Metatarsus I distinctly bent in basal half, ventral face of this curved part with three rows of short spines. Distal half of metatarsus I ventrally with a short scopula, and a less distinct scopula can be observed along tarsus I. Position of metatarsal trichobothrium on leg I ca. 0.75, between 0.65–0.7 on other metatarsi.

Male palpal cymbium with two obtuse lobes as in all known species of *Paculla* and *Lamania*. Palpal tibia thickened, but without projections. Bulbus short and wide, reniform. A very large globular seminal vesicle can be observed, but the distal part of (? short and straight) ejaculatory duct cannot be seen in the holotype specimen. Embolus basally without modifications as in all known *Paculla*, but a distally pointed laminar branch is attached ca 1/3 from the base of embolus. Copulatory orifice at the base of long distal pointed process of embolus that is continuously fringed by membranous entire lamella.

Female unknown.

Separated from all known species of *Pacullini* by type and modifications of embolus as well as by modification pattern of leg I.

The placement of this species into *Paculla*, *Lamania*, and *Sabahya* is not possible as far as their definition and delimitation follows the principles accepted in this paper. It may represent a new genus, but results achieved by analysis of evolution of different characters are somewhat contradictory. It is possible that synapomorphies and parallelisms within *Pacullini* are not totally understood yet, and that widening of some of the present genera must be accepted later.

The branched embolus, well developed

spinulation of leg I in male and the general shape of preanal plate suggest an unspecialized branch of *Sabahya*, if at least some of these similarities represent true synapomorphies. The type and general shape of embolus as well as unmodified type of cymbium and palpal tibia refer to *Paculla*, but these characters seem to be symplesiomorphies. The structure of granules on carapace and sternum is similar to all species of *Lamania*, but again this character is surely plesiomorphic. The complex and surprisingly uniform type of embolus seems to be good synapomorphy for *Lamania*, thus definitely excluding "*P.*" *cameronensis* from that genus.

Three samples of juvenile or subadult specimens were collected in areas where no adult specimens were found. At least some of them may represent new species, but they are not named here.

A short survey of the juvenile characters of *Pacullinae* is necessary before discussing the phylogenetic relationships of these unnamed species.

The abdomen is mainly sclerotized only in adult stage. Only the anal plate, a ring around petiolus as well as minor areas around the anterior spiracula and the genital orifice of both sexes are more or less heavily sclerotized at least three molts before the adult stage. In addition to this, the final contour of lateral and dorsal scuta is visible as distinct folds in the soft skin in last two subadult stages. Besides this, female specimens of *Sabahya kinabaluana*, and much less distinctly also the male subadult specimens of this species, bear paired sclerotized fields in central part of the pulmonary plate. The postgenital and preanal plates of all genera studied are completely unsclerotized in subadult specimens. Subadult males can be separated from females two molts before adult stage, when palpi are still not thickened, by more compact sclerotization around a shorter genital slit, corresponding to the final genital orifice.

The granulations and pits of carapace have the final pattern in the subadult stages, but they are less conspicuous. However, the shape of the swollen margin of the pits is exactly the same as in adult specimens.

The granulations and pits of sternum

gradually increase with each molt, and they are less numerous than in adult still in the subadult stage. As in carapace, the type of pits remains the same. The sternal apophysis is still quite insignificant in subadult stages.

In species with paired thoracic horns (checked for *Lamania nirmala* and *Sabahya kinabaluana*), these structures are distinctly visible at least in last two subadult stages, but are relatively shorter. The shape of the carapace and relative size of eyes seems to be unaltered in all juvenile stages studied, but the relative height of the cephalic area is much lower in juvenile and first subadult stages.

The presence of cheliceral teeth between the base of fang and the cheliceral lamina is unaltered in all stages studied.

The relative length of legs is always slightly shorter in juvenile specimens, and the position of metatarsal and tibial trichobothria is more basal, but the relative thickness of various leg segments is not significantly altered.

Pacullini sp. 1

One subadult specimen (? ♀) from Indonesia, Sulawesi Utara, Minahassa area, Tonsa district, Gunung Klabat (1000 m), in jungle litter, 21.X.1979, PTL, in MZT (Turku).

Medium-sized (total length 3.5 mm, carapace 1.92×1.26 mm) paculline spider with relatively long carapace and marginally quite sparsely spaced granulations. Cephalic area with longitudinal rows of starlike granulations as *Sabahya* and *Paculla*, margins of thoracic area sparsely with small teeth (cf. also *Brignoliella* spp. in Tetrablemmineae), but rest of thoracic area laterally without granulations or pits. Posterior face of thoracic area with a few granules. Position of Tmt I 0.65.

Eyes smaller than in any species of *Pacullini* known to me. Cheliceral tooth wide, clypeus with numerous hairs. Sternum relatively longer than in all known *Paculla*. Lateral abdominal pattern represented by 4 folds, posterior folds five.

This specimen is easily differentiated from known *Pacullini* species by long carapace, small eyes, and smooth parts of the thoracic area. It is further separated from *Perania* spp. by an obviously well-developed pattern of lateral and posterior scuta (folds). Adult specimens of this species are certainly larger than any of the unarmed species of Malaya. From Celebes, only *Lamania sheari* is known except for this specimen, and nothing can be

said about their relationships (cf. p. 21), but the long distance between their known localities suggests that they are not conspecific. The generic affiliation of this specimen cannot be settled according to information available now.

Pacullini sp. 2. (? *Sabahya* sp.)

Two juvenile specimens (at least three molts before adult stage) from Indonesia, Bali, Buleleng district, Danau Buyan, Pandjasari (1800 m), on moist *Marchantia* in sandy wall of cloud forest, 10.X.1979, PTL, in MZT (Turku).

Small (2.0 mm) juvenile specimens with relatively short carapace (1.1×0.8 mm). Profile of carapace very flat, type of granulations on carapace and sternum starlike. Cheliceral tooth distinct.

Abdominal sclerotizations represented only by the anal plate, areas of petiolus, anterior spiracula, and genital pore, as well as a pair of plates in posterior part of the pulmonary plate region, corresponding to pattern known only for juvenile specimens of *Sabahya kinabaluana*. No traces of paired horns in thoracic area.

Most probably a representative of the genus *Sabahya*.

Pacullini sp. (? *Paculla sulaimani*)

One subadult specimen from Malaysia, Johor, Kota Tinggi district, Jalan Lombong, Biological Field Station, in rain forest by pitfall trapping 31.X.—4.XI.1976, PTL, in MZT (Turku).

When compared with adult specimen of *Paculla sulaimani* nothing is found to exclude their conspecificity. Especially characteristic are the shape and rugosity pattern of the carapace, the long slender legs, and the small size (carapace 1.3×1.05 mm). However, altogether four species of *Pacullini* are known from more northern parts of the Malayan Peninsula and three species of *Peraniini* from the neighbouring island of Sumatra. Almost every new sample from this main speciation centre of *Pacullinae* seems to represent a new species. Thus this specimen from southern Malaya may equally well belong to a related species of *Paculla*.

Tetrablemmineae O. Pickard-Cambridge, 1873

For a complete list of synonyms and placing of tetrablemmine species, see Table 2 on p. 11. This paper presents a previously unpublished

delimitation of Tetrablemmineae, although Brignoli (1973 & 1974) has presented a classification of these armoured spiders as a single family Tetrablemmidae, divided into two subfamilies, *Pacullinae* and *Tetrablemmineae*, parallel to the present classification in regard to the numbers and names of the subfamilies concerned.

Shear (1978) delimited his family Tetrablemmidae exactly as the subfamily Tetrablemmidae is delimited here, but he divided it into two subfamilies. Tetrablemmineae (sensu Shear, 1978) and Brignoliellinae. In fact, there are only minor differences between Brignoli's and Shear's Tetrablemmineae (position of *Ablemma* and "*Hexablemma*" *castaneum*). Shear's rearrangement was due to choice of only a single character for construction of cladograms, combined with a false hypothesis about the polarity and exact homology of this character (size and position of the female genital orifice). Careful analysis of the evolution of all diagnostic characters of Tetrablemmineae (=Tetrablemmidae sensu Shear) and abundant additional material from the Old World, including representatives of several genera unknown to Shear, have revealed that there are five or more phylogenetic groups of about the same categorical rank that cannot be classified into a bifurcate scheme. The size and position of the female genital orifice is variable within three of these groups, even within the type genus of Shear's Brignoliellinae. The only consistent solution has been the creation of tribes, the most common and often quite useful auxiliary taxonomic category above the generic level.

The delimitation of these five tribes, Fallablemmiini, Brignoliellini, Ablemmiini, Tetrablemmiini, and Mattini is discussed in detail in connection with their definitions. The genera *Maijana* and *Monoblemma* could not be placed, and the position of some insufficiently known "*Monoblemma*" spp. is also obscure. The three first tribes roughly correspond to Shear's Brignoliellinae and the rest to Shear's Tetrablemmineae, but at least the former group is not monophyletic, and as such these two groups are not suitable as taxa.

For definition and differential diagnosis, see Table 1.

Fallablemmiini, tribus n.

Two mainly plesiomorphic genera from Old World, *Afrolemma* and *Fallablemma* are treated here as the tribe Fallablemmiini. Externally they resemble the most plesiomorphic genera of Brignoliellini, *Indicoblemma*, *Singaporemma*, and *Chavia*, but these similarities are all undoubtedly due to symplesiomorphic characters: eye pattern, reticulate sternum, paucity of sexual dimorphism, and simple type of external genital organs. These two groups also share an internal vulval character, presence of central apophysis that is absent in the more advanced genera of Brignoliellini. Even this character is regarded by me as symplesiomorphic. Secondary reduction of the central branch of the inner vulval plate has certainly taken place independently in several lines of tetrablemmid evolution (*Shearella*, *Maijana*).

Phylogenetically most important characters of Fallablemmiini are present in the vulval structure. The presence of a long tripartite inner vulval plate is shared with all tetrablemmine tribes with compact eye group. This structure may even be apomorphic for all these groups, but its secondary reduction in Brignoliellini is equally possible.

The sclerotization of central parts of vulva is unique in Fallablemmiini. The vulval stem does not surround the branching point of the soft vulval ducts, but there are rounded lateral plates and a central connecting plate ventrally supporting the ducts. The central process is modified in both genera, but in different ways.

The bulbous of all known Fallablemmiini is basally very wide, rounded conical, and the simple embolus is abruptly bent upwards.

The eye pattern of Fallablemmiini actually consists of a strongly recurved row, and as such this pattern may be regarded synapomorphic when compared with the plesiomorphic slightly deviating pattern in *Indicoblemma* and *Singaporemma* (and also all *Pacullinae* and *Brignoliella*).

The male chelicerae are strongly widened in *Afrolemma*, while the small anterior tooth in both genera may be homologous with the large horn on the anterior face of most Brignoliellini and topographically correspond-

ing modifications in other tribes. Thus these tooth may represent only a plesiomorphic character or a common trend in male cheliceral modification of Tetrablemmidae, rather than proof of common origin with Brignoliellini.

In spite of small number of known species, *Fallablemma* has a very wide distribution in Old World tropics, and also the range of some species (*Fallablemma greeni*, *Afroblemma thorelli*) seems to be wider than those of the majority of other Tetrablemmids. This may refer to old age of this group.

Afroblemma gen. n.

Paculla, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 189, not *Paculla* Simon, 1887.

Monoblemma, Shear, 1978. Amer. Mus. Novit. 2650: 23 (in part), not *Monoblemma* Gertsch, 1941.

Type-species *Paculla thorelli* Brignoli, 1974 from Angola.

Minute (0.95–1.2 mm) tetrablemmid spiders with fairly low, unmodified carapace in both sexes. Eyes in recurved row as in *Fallablemma*, but relative length of the eye region smaller. Male chelicerae wide, divergent, with insignificant longitudinal ridge ending in a small tooth close to the fang, cheliceral lamina exceptionally large. Surface of both carapace and abdomen more or less smooth.

Male palpal bulbous rounded conical, basally wide. Short and simple embolus bent strongly forwards. Female epigynal orifice large, subcircular, close to the posterior margin of pulmonary plate. Vulva with tripartite inner vulval plate, thin, saclike central process, and ventral, distally rounded plates supporting the basal parts of soft ducts.

Postgenital plate narrow, preanal plate oval, without modifications. First pair of lateral scuta without modifications. First pair of lateral scuta anteriorly connected with a row of small plates bearing a hair.

At least two African taxa are known, treated here as subspecies. More specimens of *A. thorelli* collected than any other tetrablemmid species, and most probably several additional species or subspecies will be found in Africa, because the African tetrablemmid fauna is very poorly known.

Brignoli (1974:190) suggested that these spiders have a spermatophore instead of the typical mode of copulation. This opinion is based on strands of coagulated liquid (? sperm) observed by Brignoli (1974: figs. 37 & 41) hanging from the tip of embolus in *A. thorelli*. Similar strands have been observed by myself

in various tetrablemmid species (Figs. 63, 117 & 175), but they may simply represent liquid sperm coagulated by the preserving fluid. A true spermatophore is suggested as occurring in copulation of Telemidae (Lopez 1977), and thus spermatophores may be possible in other haplogyne groups.

Afroblemma t. thorelli (Brignoli, 1974), comb. n.
Figs. 44–45, 50, 55 & 60–61. Table 3.

Paculla thorelli Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 189, figs. 36–37, 40, 43–44.
Monoblemma thorelli, Shear, 1978. Amer. Mus. Novit. 2650: 23.

Holotype ♂, an alloparatype ♀ from Angola, Dundo, River Luachimo, under dead leaves, 25.11.1948, Antonio de Barros Machado, in MD (Dundo), not examined. Paratypes ♂♀ from Angola in coll. P. Brignoli, examined. Abundant material from Angola listed by Brignoli (1974).

Male 1.0 mm, female 1.2 mm, both sexes described in detail by Brignoli (1974), but he did not mention the cheliceral modification in male. The vulval structure deserves following additional remarks. The central process is not sclerotized, but consists of a large soft sac, attached by a long duct dorsally behind the base of soft vulval ducts. The thin inner vulval plate is obviously originating dorsal to this process, but only the distal part of the unpaired branch is visible in cleared specimen. The sclerotized lateral processes of the vulval stem support ventrally and posteriorly the vulval ducts, and their distal parts seem to constitute complicated sclerotizations along the surface of the receptacula.

Colouration of both sexes light yellowish brown, all chitinous surfaces practically smooth.

Differentiated from geographically quite distant species of *Fallablemma* by smaller size, yellow colouration, and smooth surface, as well as wide, divergent chelicerae in male and different type of genital organs in female. Cannot be confused with any other known African tetrablemmids. The placing to *Monoblemma* by Shear (1978) is hard to understand.

Afroblemma thorelli maniema ssp. n.

Paculla prop. *thorelli*, Brignoli 1974. Publ. Cult. Comp. Diam. Angola 88: 191, figs. 38–39, 41–42.

Holotype ♂ from Zaire, Maniema, between Kampene and Kamituga, in bamboo forest, 20.VIII.1955, Antonio de Barros Machado, in MD (Dundo), not examined. Both sexes listed from a few localities from Zaire (Brignoli 1974).

Male 1.18 mm, female 1.28 mm. Male palpus thicker than in *A. t. thorelli*, bulbous distally without

constricted apex, embolus relatively shorter. A more detailed description presented by Brignoli (1974). The differences between *A. t. thorelli* and *A. t. maniema* could be sufficient for specific status, but the infraspecific variation of both taxa is imperfectly known and the original description mentioned the presence of both forms in the same area. Thus, according to principles adopted for this paper, *A. t. maniema* is listed as a distinctly allopatric subspecies until more information about morphological variation of this and related taxa will be available.

Shear (1978) listed a female of his *Monoblemma thorelli* from Tanzania. This specimen may represent an additional taxon of *Afroblemma*.

Fallablemma Shear, 1978

Hexablemma, Marples, 1955. J. Linn. Soc. London 42: 460 Pl. 56: figs. 1, 2 & 17, not *Hexablemma* Berland, 1920.

"*Hexablemma*", Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 83, not *Hexablemma*, Brignoli, 1974 or 1978.
Fallablemma Shear, 1978. Amer. Mus. Novit. 2650: 29.

?*Hexablemma* sp., Shimojana, 1977, Acta Arachnol. 27: 362.

Type-species by original designation and monotypy: *Hexablemma castaneum* Marples, 1955 from Samoa.

Small (0.95–1.3 mm) tetrablemmid species with unmodified carapace in both sexes, but cephalic area ending in a pointed tooth. Eye region large, eyes in strongly recurved row. Male chelicerae unmodified, except a small denticle on the anterior face, close to the base of fang. Carapace smooth, microsculpture quite finely reticulate. Sternum coarsely reticulate, pulmonary plate undulate and with small pits for hairs. Postgenital plate laterally tapering, preanal plate rounded at anterolateral corners, without pits in both sexes. Lateral scutum I extending to the postgenital plate, continued with a few small plates.

Male palpal femur long, unmodified, patella very short. Palpal tibia long and swollen. Palpal bulbous relatively very large, short pear-shaped. Embolus strongly bent forwards as in *Afroblemma*.

Epigynal fold narrow, epigynal pit small, transversely oval on top of median projection of the pulmonary plate. Vulval stem strongly sclerotized dorsal to the vulval ducts, its lateral horns distally rounded, situated dorsal to the ducts. Anterior margin of vulval stem with paired, diverging sclerotized strips attached to the inner surface of the pulmonary plate. This paired structure may be homologous with the central process of most Tetrablemmidae, but does not have any secretory functions as the central process of related *Afroblemma*. Inner vulval plate with basal transverse part and long, narrow central branch as most Tetrablemmini.

Two species known from Celebes and Samoa, both living in leaf litter of forests, but a third probably occurs in Ryukyu Islands.

Fallablemma castaneum (Marples, 1955)

Hexablemma castanea Marples, 1955. J. Linn. Soc. London 42: 460 Pl. 56: figs. 1, 2 & 17.

Fallablemma castaneum, Shear, 1978. Amer. Mus. Novit. 3650: 31, figs. 77–80 (including emendation of the specific name).

Male and female syntypes from Samoa (Upolu, Manono & Apolima) 1945–1951, B. J. Marples, in BMNH (London), examined in 1977, lectotype not selected.

Marples (1955) described both sexes in detail, but there is a contradiction between his measurements, especially those of the male. A total length of 1.15 mm for the female is probably correct. Shear (1978) gave additional information on both sexes, including accurate SEM micrographs concerning the male palp. According to this, *F. castaneum* is in all respects close to *F. greeni*, but the palpal bulbous is relatively smaller and longer. The females have not been compared side by side, but *F. castaneum* seems to be smaller than *F. greeni*.

Fallablemma greeni sp. n. Figs. 33, 40, 42, 53, 59 & 63. Table 3.

Holotype ♂, alloparatype ♀, and 18 ♂ 10 ♀ 1 juv. from Indonesia, Sulawesi Tengah, Tawaeli district, Toboli road, W of Karupua, in litter of mountain forest (300 m), 26.X.1979, PTL, in MZT (Turku).
Sulawesi Utara, Gorontalo district, Databu (600 m), in litter of jungle slope with Araceae, 24.X.1979, PTL: 5 ♂ 9 ♀. — Minahassa area, Tonsa district, Gunung Klabat (1500 m), litter of palm jungle, 21.X.1979 PTL, Kathleen Steerman & James Greene: 3 ♂, 6 ♀.

Male 1.15–1.2 mm. Clypeus higher than in female, but without any modifications. Posterior corner of the cephalic area distinctly pointed. Eyes quite pale, subcircular, not touching, ALE>PME>PLE, but size differences insignificant. The whole surface of the carapace very finely reticulated, more distinctly in clypeus and around the margins. Cheliceral denticle very small, fairly lateral in position, and best seen in profile.

Dorsal abdominal scutum oval, densely pitted and hairy.

Palpal tibia strongly swollen, bulbous very large. Female 1.25–1.3 mm. Clypeus lower than in male, posterior corner of the cephalic area as distinct as in male. Basomedian knob of the chelicerae more strongly developed than in male, but the distal denticle absent.

Epigynal area distinctly bulging backwards, epigynal pit small. Vulval sclerotizations usually visible through the integument.

There is no variation between populations from described species of *Fallablemma*.

Fallablemma sp.

Hexablemma sp., Shimojana, 1977. Acta Arachnol. 27: 362.

Shimojana (1977) listed a *Hexablemma* sp. from Ryukyu Islands, Iriomote Jima, Nakano-do Cave, 29.V.1974, found together with *Ablemma shimojanai*. This species was mentioned separately among the five new species found under that survey of cave spiders, but no description was presented and no drawings given.

The species was mentioned with reference to presence of a *Hexablemma* in Samoa. Judging from the presence of a common species of this Samoan genus (*Fallablemma*) in Celebes, I believe that the specimen from Ryukyu Islands represents an undescribed species of *Fallablemma*.

Brignoliellini, tribus n.

The subfamily Brignoliellinae Shear, 1978, is not monophyletic, but there is a natural group of tetrablemmids around the type genus, *Brignoliella*. It is regarded here as a tribe, and there are most probably many more undescribed than known species. The species of this tribe are ecologically similar, living in litter and moss of tropical forests. Many of them belong to the dominant spider species of the litter fauna, especially in Indonesia and neighbouring areas. The total range of Brignoliellini extends from Himalaya and Ceylon to the Philippines and Micronesia. The most plesiomorphic genera are the most western in distribution.

The phylogenetic relationships of Brignoliellini are not exactly known. The most plesiomorphic genus, *Indicoblemma*, is externally fairly similar to all species of Fallablemmi, but the structure of genital organs reveals that they belong to different evolutionary lines. However, Brignoliellini is obviously more closely related to Fallablemmi than to any other tribe of Tetrablemmiinae.

The tribe Brignoliellini now comprises 32 known species, classified into seven genera, *Indicoblemma*, *Chavia*, *Choireblemma*, and *Singaporemma* (all with reticulate sternum), *Pahanga*, *Borneomma*, and *Brignoliella* (all with pitted sternum). The three last genera are divided into well defined groups. Some of these groups are treated here as subgenera,

while deviating groups represented by females only are consistently treated otherwise.

Brignoliellini is characterized by several morphological characters, both plesiomorphic and apomorphic. All its species have retained the basic eye pattern of Sicarioidea. There is a strong tendency towards pitted structure of all ventral plates, including the sternum. However, *Indicoblemma* and *Choireblemma* are without pits in all ventral scuta, and *Chavia* has a strongly pitted pulmonary plate, but a reticulate sternum. *Singaporemma* represents a deviating type in this respect, being strongly reticulate in all sclerotized plates, including the postgenital and preanal plates. For the rest of genera, a strongly pitted sternum is an excellent key-character. The pitted structure is extended also to some parts of carapace in many species of *Pahanga* and *Brignoliella*. Various pitted pulmonary plates are present also in some species groups of Ablemmi, Tetrablemmi, and Mattini. The margins of the carapace are more or less serrate in all species of *Pahanga*, *Borneomma*, and *Brignoliella*. The apomorphic modifications of the sclerotized plates seem to be correlated with each other.

The legs are unmodified in both sexes, and the males have only slightly longer legs than the females of the same species.

The sexual dimorphism of the male always includes cheliceral modifications in the anterior surface, but they may be parallel to some less striking modifications in Fallablemmi and Mattini. The sexual dimorphism in the male carapace is usually present in Brignoliellini, but it does not affect the eye pattern (cf. Ablemmi and most Tetrablemmi). The males of Brignoliellini either have modifications in the clypeus (*Choireblemma*, *Borneomma*, *Brignoliella*) or at least a slightly different profile (*Indicoblemma* & *Pahanga*). There is no sexual dimorphism in non-genital characters of *Singaporemma*.

The male palpus of Brignoliellini is usually plesiomorphic in regard to most details, but a "conductor" (well defined projection of bulbus) has developed independently in *Choireblemma*, *Borneomma* s. str., and *Brignoliella* (*Diploblemma*). The subglobular shape of the bulbus is characteristic for most groups within Brignoliellini, but it is not a key-character

even for single genera or subgenera of *Brignoliella*. Embolus is terminal except in *Singaporemma* and without significant basal or distal modifications.

In contrast to information given by Shear (1978) for *Brignoliella*, the epigyne of this tribe is not of uniform type. Many species have a large epigynal pit, distinctly anterior to the margin of the pulmonary plate, but the epigynal pit of *Pahanga*, *Choireblemma*, *Singaporemma* and many species of *Brignoliella* is very insignificant. The large epigynal pit in Ablemmi and some Fallablemmi (*Afroblemma*) is superficially quite similar to the most common epigynal type of Brignoliellini, although the internal structures are different.

The vulva of Brignoliellini is always diagnostic in spite of various parallel modifications of other characters. There is no well-defined vulval stem and no sclerotized lateral horn. In its simplest form, the vulva of Brignoliellini constitutes only of an unpaired duct as a direct continuation of the genital orifice and two soft branches leading to the saclike receptacula. The branching point may be variously sclerotized, and the most plesiomorphic genera (*Indicoblemma*, *Chavia*, *Singaporemma* and *Choireblemma*) have a simple central process. The inner vulval plate of all Brignoliellini is a simple transverse bar. This is a useful key character in separating species of Brignoliellini from Ablemmi or most Tetrablemmi (with trifurcate inner vulval plate).

The preanal plate of female Brignoliellini is usually with paired furrows or pits to fit the male cheliceral modifications. Preanal pits are also present in most Ablemmi, but they are posterolateral or posterior in position, while most of the females of Brignoliellini have anterolateral, central, or anterior pits.

The preanal pits are absent in females of *Singaporemma* and *Chavia*, simply because of simple structure of male chelicerae.

Indicoblemma, Bourne, 1980

Type-species *I. sheari* Bourne, 1980 from Darjeeling area, India. The small paper by Bourne (1980) was published before the printing of this paper and thus names suggested by him are used here. Our correspondence was

meant to minimize possible synonyms, but through misunderstanding some names suggested by me were in vain published by Bourne (1980) in a post scriptum. These names are herewith considered junior synonyms, although published simultaneously with Bourne's names, according to the principle of first reviser. The name *Chavia* is herewith restricted to the species *C. monticola*, and it is therefore not an objective synonym of *Indicoblemma*, although it could be regarded a subjective synonym of the latter, as *C. monticola* and *I. sheari* were regarded as representatives of different subgenera of *Chavia* in first manuscript version. Now, with all additional information, these two related taxa are regarded as well argued genera. This detailed discussion is presented here to avoid any further nomenclatory confusions of *Indicoblemma* and *Chavia*. My material of the single known species of *Indicoblemma* is collected from exactly the same area, and our descriptions certainly refer to the same species.

Small yellowish brown tetrablemmids with *Brignoliella*-type of eye pattern and carapace unmodified in both sexes. Carapace and sternum reticulate. Male chelicerae and female preanal plate with *Brignoliella* type of modifications, including small anterior conical tooth in male chelicerae and a pair of oblique pits in the female preanal plate.

Male palpal tibia swollen, bulbus pyriform, embolus short and straight. Female epigynal orifice insignificant, vulval ducts thin and simple, weakly sclerotized, without separate sclerotized plates or supporting parts. Small, rounded central process present, inner vulval plate without unpaired central branch as in all known genera of Brignoliellini.

Indicoblemma is without doubt a more plesiomorphic relative of *Brignoliella*, *Pahanga*, and *Borneomma*, and probably the most plesiomorphic genus of Brignoliellini. It has an external resemblance with *Singaporemma*, but this is mainly due to the reticulate pattern of surfaces. The pattern of abdominal scuta and male palpus are largely dissimilar in these two genera, and they seem not to be close relatives, although members of a common tribe.

Indicoblemma sheari Bourne, 1980
Figs. 38, 46, 52, 57 & 65. Table 3.

Indicoblemma sheari Bourne, 1980. Rev. Suisse Zool. 87: 308, figs. 25–30.

Chavia himalayensis Lehtinen in Bourne, 1980. Rev. Suisse Zool. 87: 316. Selected herewith as the junior synonym from two simultaneously published names.

Holotype ♂ and ♀ paratypes from India, West Bengal, Darjeeling District, "entre Ghoom et Lopchu, 14.X.1978, à 13 km de Ghoom, versant nord, 2000 m. tamisage en forêt", leg. C. Besuchet and I. Löbl, in MNHG (Geneva), not examined. Additional records from Darjeeling area listed by Bourne (1980).

Own material: India, West Bengal, Darjeeling district, 1.5 km NW of Sukhiapokri (2350 m), litter of cloud forest with many stones on ground, 1.V. 1979, PTL: 1 ♂; Darjeeling district, Sunguri, close to Chittree road (2400 m), moss in coniferous forest, 1.V.1979, PTL: 1 ♀.

Male 0.85 mm. Eyes small, subequal in size. Anterior cheliceral tooth small, directed inwards. Lateral scutum I short, posteriorly represented by only a fold. Postgenital plate short, unmodified.

Male palpal tibia strongly swollen. Bulbus relatively small, embolus short, basally wide, distally tapering, almost straight.

Female 0.9 mm. Similar to male, but chelicerae without anterior tooth. Epigynal fold centrally wide, epigynal pit concealed behind it.

Chavia gen. n.

Type-species *Chavia monticola* n. sp. from northern Thailand.

Relatively large tetrablemmine spiders (1.35 mm). Carapace rounded in profile. Eyes large and close to each other, resulting in a wide recurved row. Sternum exceptionally convex, protruding, coarsely reticulate. Pulmonary plate pitted as in *Brignoliella* and related genera. Lateral scutum I represented by a dense row of small plates and a continuous anterior plate. Vulva simple, duct weakly sclerotized, no extra plates, central process rounded, unmodified. Preanal plate with anterior transverse furrows, but no pits.

Males unknown.

Chavia monticola sp. n.

Figs. 32, 39, 41, 48 & 56. Table 3.

Holotype ♀ from Thailand, Lampang Province, Doi Inthanon National Park (1800 m), in litter of cloud forest, 15.XI.1976, PTL, in MZT (Turku). A female specimen from Chiangmai province, Doi Suthep (1400 m), in dry forest slope, 14.XI.1976, was subsequently lost.

Female 1.35 mm. Six large eyes in recurved row, ALE largest. Carapace long oval, smoothly rounded in profile, surface almost smooth. Margins of cephalic area dorsally with some irregularly placed hairs, but no warts or pits present. Chelicerae basally rounded, without any traces of basal knob or other modifications.

Sternum convex, posteriorly widely obtuse. Post-

genital plate very small. Preanal plate transversely oval, without submedian pits, but anterior margin distinctly folded. Epigynal orifice represented by a central notch in the epigynal fold. Dorsal abdominal scutum densely pitted and covered with short hairs.

Channel from epigynal orifice to paired vulval duct much longer than in *Indicoblemma sheari*.

Differentiated from all other tetrablemmids by strongly convex sternum, closely spaced eyes, and rounded profile of carapace.

Choiroblemma, Bourne, 1980

Type-species *Choiroblemma bengalense* Bourne, 1980 from Darjeeling area, India.

Eyes fairly small, in three pairs much as in *Indicoblemma*. Male carapace anteriorly modified to a clypeal snout, male chelicerae with small anterior projection. Sternum reticulate. Female preanal plate with a pair of submedian pits.

Male palpal bulbus with a separate conductor. Epigynal orifice small, vulva simple with no lateral horn. Central vulval process well developed, rounded.

Described in detail by Bourne (1980). Two sympatric species from Darjeeling area known.

Choiroblemma bengalense Bourne, 1980

Holotype ♂, 1 ♂ and 3 ♀ paratypes from India, West Bengal, Darjeeling District, "Mahanadi près de Kurseong, versant sud, alt. 1200 m, 6.X.1978, tamisage en forêt". Extraction by Winkler method, leg. C. Besuchet and I. Löbl, in MNHG (Geneva), not examined.

Male 1.21 mm. Cephalic area with distally obtuse snout. Conductor basally wide, triangular.

Female without modification of carapace and chelicerae. Epigynal orifice in bulging central part of epigynal fold, copulatory channel long. Preanal plate with oblique pits.

Both sexes described in detail by Bourne (1980).

Choiroblemma rhinoxunum Bourne, 1980

Holotype ♂, 1 ♂ and 2 ♀ paratypes from India, West Bengal, Darjeeling District, Singla, 300 m, 17.X.1979. "Tamisage dans une forêt secondaire de Tecks." Extraction by Winkler method, C. Besuchet and I. Löbl, in MNHG (Geneva), not examined.

Male 1.24 mm. Carapace with conical snout. Anterior cheliceral projection blunt. Palpal conductor narrower than in *C. bengalense*.

Female without modifications in carapace and chelicerae. Epigynal orifice small, but copulatory channel shorter than in *C. bengalense*. Preanal plate with two closely spaced, curved slits.

Both sexes described in detail by Bourne (1980).

Bourne (1980) compared this genus with *Singaporemma*, but could not place it in

Shear's cladogram. In my opinion, these two species undoubtedly belong to a monophyletic taxon that is more closely related to *Indicoblemma* than to *Chavia* or *Singaporemma*. The conductor of *Choiroblemma* may be partly homologous with the conductor of *Borneomma*, but possibly not with the conductor of *Brignoliella* (*Diploblemma*) or that of various genera of Mattini. However, *Borneomma* is not a close relative of *Choiroblemma*, and their conductor cannot be interpreted as a synapomorphy, at least in the usual meaning of this term. Rather this case is a further example of discontinuous appearance of homologous structures or patterns (cf. p. 76).

Singaporemma Shear, 1978

Singaporemma Shear, 1978. Amer. Mus. Novit. 2650: 36.

Type-species by original designation and monotypy *S. singularis* Shear, 1978 from Singapore.

Small tetrablemmids (0.9–1.15 mm) with no clypeal modifications in male, but clypeus protruding. Thus ocular area is situated far from the anterior margin. Six eyes in short, recurved row. Cephalic area posteriorly raised, especially in females. Chelicerae of both sexes unmodified, the basal knob small and situated exceptionally far from the cheliceral base in median line.

Surface of carapace, sternum, dorsal scutum, and pulmonary plate coarsely reticulate. Hair covering relatively long, especially in the dorsal scutum. Postgenital and preanal plates longer than in other Brignoliellini and most groups of Tetrablemmiinae. Lateral scutum I absent throughout its whole length, while all other tetrablemmine genera have at least a short anterior plate remaining. A paired anterior plate present between lateral plates IV. Large perigenital plates present in posterior part of abdomen. Preanal plate not pitted or furrowed.

Male palpal tibia thickened, bulbus oval. Embolus originating from the mesial side of the bulbus, variable in shape.

Epigynal orifice small, in slightly bulged posterior margin of the pulmonary plate. Vulva with distinct, sclerotized copulatory channel that has rugose inner surface. Basal part of paired vulval ducts with thick, sclerotized walls, but without separate supporting plates. Central process well developed, attached to the dorsal surface of the copulatory channel with long stalk.

Three known species from Singapore to Vietnam, all living in forest litter.

Species of *Singaporemma* are compared with *Indicoblemma* and related genera because of striking symplesiomorphies, especially the

reticulate surface of sternum. Cladistically this genus is not closely related with the other plesiomorphic genera of Brignoliellini. The exact relationships of *Singaporemma* with known genera of Brignoliellini are not known, but the structure of female genital organs definitely proves that it is a member of Brignoliellini.

Singaporemma singularis Shear, 1978

Singaporemma singularis Shear, 1978. Amer. Mus. Novit. 2650: 36, figs. 108–111.

Holotype ♂ and alloparatype ♀ from Singapore, near McRitchie Reservoir, 25.X.1950, M. W. F. Tweedie, in AMNH (New York), not examined.

Male 1.02 mm, female 1.15 mm. Described by Shear (1978). Male embolus thin and bent almost to a right angle, originating from basal half of short oval bulbus. Shear (1978) emphasized the pale yellow colour of his paratype specimens, but this is certainly not diagnostic, and due to incomplete sclerotization only.

Male separated from the two vietnamese species by shape and position of embolus, differences in vulval structure of females not known.

Singaporemma halongensis sp. n.

Figs. 43, 49, 54, 58 & 62. Table 3.

Holotype ♂, alloparatype ♀, and additional paratypes (5 ♂ 13 ♀ 3 juv.) from Vietnam, Quang Ninh, Ha Long, in litter of brook valley at 30 m, 11.X.1978, PTL, in MZT (Turku); Ha Long (40 m), from jungle litter, 13.X.1978, PTL: 1 ♀ 1 juv.

Male 0.92 mm. Embolus long and thin, straight distally shortly curved, originating from distal half of oval bulbus. Other characters similar to *S. singularis*.

Female 0.92 mm. Surroundings of genital orifice strongly protruding. Externally quite similar to other species of *Singaporemma*. Copulatory channel much narrower than in *S. adjacens*. Central vulval process distally rounded.

Singaporemma adjacens sp. n.

Figs. 47, 51 & 64. Table 3.

Holotype ♂, alloparatype ♀ and 1 ♂ 2 ♀ paratypes from Vietnam, Quang Ninh, Ha Long, in litter of dense jungle close to seashore (10 m), 12.X.1978, PTL, in MZT (Turku).

Male 0.90–0.94 mm. Embolus consists of a wide, slightly screwed lamella which tapers towards both ends. Origin of embolus subapical in long oval bulbus.

Female 1.01–1.03 mm. Surroundings of genital

orifice not protruding, but central part of the posterior margin of epigynal fold widely obtuse. Copulatory channel very wide, central vulval process distinctly forked. Neither sex easily distinguishable from *S. halongensis* using non-genital characters, but there is no variation in genital organs within each of these sympatric species. The present material is not sufficient to demonstrate possible ecological differences, but mixed populations were not observed, although the samples of both species come from a very limited area.

Pahanga Shear, 1979

Pahanga Shear, 1979. Bull. Br. Arachnol. Soc. 4: 294.

Type-species by monotypy: *Pahanga dura* Shear, 1979 from Malaya.

Male carapace slightly raised, but without clypeal modifications. Male chelicerae with horns of various size. Male palpal femur short, curved, palpal patella lengthened. Male palpal bulbus pyriform, embolus simple, conductor absent.

Female preanal plate with unpaired posterior or paired anterior pit. Female genital orifice small, inner vulval plate wide, obtusely triangular.

Four species known, all living in forest litter from Sri Lanka to Western Sumatra and Malaya. Two other species are not closely related with the genotype, and probably subgenera or even new genera must be erected for them when unknown sexes of all species will be found.

Pahanga dura Shear, 1979

Pahanga dura Shear, 1979. Bull. Br. Arachnol. Soc. 4: 295, figs. 1—4.

Holotype ♂ from Fraser's Hill, ca. 1300 m elevation, from Malaysia, Pahang, 16.IV.1967, W. L. Brown, in MCZ (Cambridge), not examined.

Male 1.46 mm, anterior cheliceral horns large, resembling those of the species included here in the genus *Shearella*. Palpal bulbus elongate pyriform, embolus short, strongly curved. A detailed description presented by Shear (1979). Female unknown.

Differentiated from *P. lilisari* by much larger cheliceral horn, relatively longer palpal bulbus, and shorter embolus. Separated from females of other species, including the sympatric *P. centenialis* by much larger size.

Pahanga lilisari sp. n.

Figs. 67, 69, 78, 79 b & 81—82. Table 3.

Holotype ♂, alloparatype ♀, and additional paratypes (14 ♂, 10 ♀, 3 juv.) from Indonesia, Sumatera Barat, District Padangpanjang, Lembah Anai, 4 km SW of Padangpanjang, moist jungle slope with leaf litter at 900 m, 26.IX.1978, PTL, in MZT (Turku).

Male 1.3—1.35 mm. Carapace and especially

cephalic area wider than in most species of Brignoliellini, except *Borneomma* spp. Cephalic area surrounded by irregular rows of hairs, originating from fairly large pits. Thoracic area gently sloping from cephalic area, completely rugose due to continuous granules. Clypeus high, but without horns or modifications. Eyes large. Chelicerae with narrow, laminar processes, touching in median line, and obviously fitting into the unpaired pit in the preanal plate of female. Origin of these cheliceral processes at the base of the cheliceral lamina, thus in the apical half of the chelicerae. Sternum with large concavity posteriorly, completely densely pitted with large pits as in *Brignoliella michaeli* or *Borneomma roberti*.

Abdomen oval, dorsal scutum densely pitted and hairy, pulmonary plate also densely pitted. Other ventral plates as in *Brignoliella* spp. First lateral scutum entire, but quite narrow.

Male palpal femora short, basally strongly thickened, palpal patellae greatly enlarged, resembling the palpal tibia in length and shape. Bulbus large, short pyriform, embolus is a simple curved spine.

Female 1.35—1.4 mm. Carapace lower than in the male, chelicerae unmodified. The preanal plate with an unpaired, semicircular pit close to the posterior margin, anterior margin with a continuous groove. Postgenital plate anteriorly strongly convex, with internal fold opposite the genital pore at the posterior margin of the pulmonary plate. Epigynal pore insignificant, inner epigynal plate transverse, but central part wider, resulting in total shape of very wide, rounded obtuse triangle.

Differentiated from *P. dura* by type of cheliceral horns and details of bulbus, from other species of *Pahanga* by much larger size.

Pahanga diyaluma sp. n.

Figs. 68 & 79 a. Table 3.

Holotype ♀ and one paratype ♀ from Sri Lanka, Moneragala District, Diyaluma Falls, in litter of dense, dark jungle, 18.I.1969, PTL, in MZT (Turku).

Female 1.3 mm. Carapace, chelicerae, and abdomen dorsally much as *P. lilisari*, and also resembles all other females of Brignoliellini. Cephalic area ends in a small tooth, best seen in profile. ALE eyes large, PME separated from each other as well as from ALE by ca. half diameter. Clypeus strongly pitted. Sternal pits fairly small, but sparsely distributed. Hairs of dorsal scutum short. Postgenital plate narrow, practically vertical. Preanal plate with paired grooves in lateral thirds of the anterior margin.

Female genital pore circular, distinct, but smaller than in *Brignoliella* spp. with subcircular pore. Male unknown.

Differentiated from *P. centenialis* by large genital pore, but otherwise very close to this species. Separated from all other females of Brignoliellini by position of the grooves or pits in the preanal plate, as well as by strongly pitted clypeus (cf. "*B.*" *sarawak* and *B. maros*.)

Pahanga centenialis sp. n.

Figs. 66, 76—77 & 86. Table 3.

Holotype ♀ with a broken paratype ♀ from Malaysia, Selangor, Templer Park, Hutan Simpang in jungle litter, 20.XI.1979, PTL, in MZT (Turku).

Female 1.13 mm. Carapace, chelicerae, sternum, abdominal scutum, and legs similar to those of *P. diyaluma*. Anterior grooves of the preanal plate as in *P. diyaluma*, but the anterior margin of preanal plate more convex.

Female genital pore very small and insignificant, but the epigynal area is characterized by a whitish V-shaped swelling, penetrating under the folded posterior margin of the pulmonary plate. Male unknown.

Differentiated from *P. diyaluma* by differences in genital area and slightly smaller size.

The placing of *P. diyaluma* and *P. centenialis* into *Pahanga* is only provisional and their exact position cannot be confirmed without males. They can definitely be excluded from both *Borneomma* and *Brignoliella*, and they may represent a new genus. In spite of pitted clypeus, they do not seem to be closely related to "*Brignoliella*" *sarawak*.

Borneomma Deeelman-Reinhold, 1980

Type-species *Borneomma roberti* Deeelman-Reinhold, 1980 from Borneo.

Male carapace high, clypeus with a smooth transverse elevation immediately below the eyes. Male chelicerae with small, blunt, basal tooth. Cephalic area of male widened. Male palpus with or without conductor. Female preanal plate with central furrows. This definition is not identical with the original one by Deeelman-Reinhold (1980), because an additional species, *B. (Oleoblemma) yuata* is included in the same genus.

Known distribution restricted to Borneo.

Borneomma (Borneomma)

Deeelman-Reinhold, 1980

Palpal bulbus with a conductor. Paired pits in the preanal plate of female close to the anterior margin.

Borneomma (B.) roberti Deeelman-Reinhold, 1980

Figs. 72—73 & 85. Table 3.

Holotype ♂ and paratype ♀ from National Park Kinabalu, Sabah (Malaysian Borneo), Head Quarters at 1550 m, by sieving leaf-litter of rainforest, 26—29.VI.1979, leg. P. R. Deeelman and C. L. Deeelman, in RMNH (Leiden), not examined. 3 ♂

2 ♀ paratypes with same data also mentioned in the original description.

Own material: Malaysian Borneo, Sabah, Tuaran district, Mt Kinabalu National Park, Silau Silau trail, in litter of rain forest at 1450 m, 10.XI.1976, PTL, in MZT (Turku): 1 ♂.

Male 1.3 mm. Carapace very high, but short, clypeus with a large elevation below the eye group. Cephalic area wide, horizontal, surrounded by an irregular row of hairs originating in distinct pits. Upper third of thoracic area vertical, lower parts steeply sloping. Sternum densely pitted, pits as large as in *Brignoliella michaeli*.

Abdomen long oval, but petiolus close to the centre. Thus posterior part of the pulmonary plate much wider than long. Postgenital plate exceptionally large, preanal plate narrow, resulting in only small difference in the size of these plates. Lateral scutum I long, extending posteriorly as far as the preanal plate, perigenital plates minute. First tarsi spindle-shaped.

Palpal femur and patella unmodified, palpal tibia slightly thickened. Bulbus large, obtusely pear-shaped, embolus falciform, its base transversely widened. Conductor hook-shaped, originating distinctly separate from the base of embolus, much lighter in colour.

Female 1.4 mm, described in detail by Deeelman-Reinhold (1980). Non-genital characters obviously similar to *B. yuata*, position of the paired pit of the preanal plate more anterior. Epigynal pit insignificant, vulva possibly more weakly sclerotized than in *B. yuata*.

Separated from *B. yuata* by details of male and female genitalia.

Borneomma (Oleoblemma), subgen. n.

Type-species *Borneomma (Oleoblemma) yuata* sp. n. from Borneo.

Palpal bulbus without conductor. Paired pits in the preanal plate of female far from the anterior margin of this plate.

Borneomma (Oleoblemma) yuata sp. n.

Figs. 70—71, 74—75 & 83—84. Table 3.

Holotype ♂, alloparatype ♀, and additional paratypes (3 ♂ 6 ♀ 1 juv.) from Indonesia, Kalimantan Timur, Bulungan district, Tarakan Island, Yuata, in wet palm jungle at 10 m elevation, 1.XI.1979, PTL, in MZT (Turku). 6 ♂ 4 ♀ paratypes from Tarakan Island, Simpangan Sasani, in jungle litter, 1.XI.1979.

Male 1.0—1.05 mm. Cephalic area posteriorly widened, almost heart-shaped, smooth, and fringed by a dense row of hairs. All other parts of carapace finely reticulated. Clypeus high, ca. five times the diameter of ALE, concave. A pair of rounded elevations below the eyes. Eyes relatively large, ALE slightly larger than the other pairs of eyes, median eyes circular. Chelicerae very short and wide, basal rounded teeth similar to those of *B. roberti*.

Dorsal abdominal scutum short oval, densely pitted. Sternum sparsely pitted, pits slightly smaller than in *B. roberti*. Pulmonary plate densely pitted with much smaller pits. Posterior part of pulmonary plate twice as wide as long, preanal plate narrow as in *B. roberti*, but postgenital plate relatively much narrower. Lateral scutum I contiguous with the anal plate. First tarsi spindle-shaped, relatively more swollen than in the preceding species.

Basal segments of the male palpus normal, palpal tibia thickened. Bulbus subglobular. Embolus short, almost straight spine, basally wide. Conductor absent.

Female 1.05–1.1 mm. Cephalic area long oval, slightly widened posteriorly, posterior margin centrally with a small tooth as in females of *Pahanga*. Carapace much lower than in male, resembling in profile that of other females of this tribe. Chelicerae and first tarsi unmodified, shape of abdominal scuta as in male. Preanal plate with a T-shaped central ridge, flanking paired submedian pits. Legs distinctly shorter than in male, and also shorter than in most other species of this tribe, except *Brignoliella maros* and *B. vulgaris*. The femora of first leg are relatively shorter than in any other species.

Epigynal area characterized by the very large, obtusely triangular folded margin of the pulmonary plate. This fold is centrally dark, and this dark part covers the small epigynal orifice. Bases of dark receptacular ducts shine through the integument and point slightly backwards. The inner vulval plate is simple, transverse.

This species is easily differentiated from *B. roberti* by absence of conductor, but also in different shape of the cephalic area, and the females can be separated from the females of the latter species by different pattern and shape of ventral abdominal plates. The males are further separated from all *Brignoliella* spp. by lack of clypeal horns and from *Pahanga* spp. by unmodified palpal femora and patellae, as well as by the shape of bulbus. The female preanal plate with central ridge is different from all species of this tribe.

The creation of a new genus with two monotypic subgenera is a somewhat exceptional taxonomic solution. However, this case can be well argued. The relationship of *B. roberti* and *B. yuata* seems to be certain due to several synapomorphies, but the presence of a conductor in the first species reveals that they are not too closely related. Both of them have most probably several living relatives, as the small ground spiders of the Indonesian islands are still very imperfectly known.

Brignoliella Shear 1978

Polyaspis Simon, 1889. Ann. Soc. Entomol. France (6)8: 244. Junior homonym of *Polyaspis* Berlese, 1888.

Paculla, Simon, 1893. Ann. Soc. Ent. France 62: 324, not Simon 1887.

Paculla, Simon, 1894. Hist. Nat. Aragn. 1(3): 569, figs. 577–581 (*Polyaspis* = *Paculla*).

Paculla, Roewer, 1963. Insects of Micronesia 3(4): 127, figs. 9 a–d.

Paculla, Brignoli, 1973 (in part). Mem. Soc. Entomol. Ital. 52: 82, not *Paculla*, Brignoli, 1972, 1974, 1975 or 1978.

Brignoliella Shear, 1978 as a *nomen novum* for *Polyaspis* Simon, 1889. Amer. Mus. Novit. 2650: 24.

Brignoliella, Bourne, 1980. Rev. Suisse Zool. 87: 302 & 306.

Brignoliella, Deeleman-Reinhold, 1980. Zool. Meded. 56:79.

Type-species of *Polyaspis* Simon, 1889: *P. acuminata* Simon, 1889 from New Caledonia, by monotypy.

Type-species of *Brignoliella* Shear, 1978: *Polyaspis acuminata* Simon, 1889, according to ICZN (1964 § 67 (i)).

Small (1.1–1.9 mm) tetrablemmid spiders with paired or lobed horn in the male clypeus. Male chelicerae with 1–3 central processes of variable size and shape on the anterior face. Male palpal femur, patella, and tibia unmodified, palpal bulbus flattened spherical to pear-shaped, embolus slightly modified or unmodified, terminal in position. Conductor usually absent, but present in one group.

Female preanal plate with paired pit or furrow in variable positions. Epigynal pit variable in size, but usually distinct, and situated anterior to the margin of pulmonary plate. Central process of vulva totally reduced, branching point of vulval ducts variously sclerotized, but without lateral horns.

Legs of both sexes without modifications, relatively longer in males.

The nomenclatorial history of this large and locally dominant tetrablemmid genus is confusing because Simon (1893 & 1894) synonymized his own *Polyaspis* with *Paculla* without examination of any specimens of the latter genus. This error was then accepted by many later Tetrablemmid specialists, again because they had seen no specimens of *Paculla*.

My concept of *Brignoliella* is slightly different from that of Shear (1978), mainly because many more specimens of Brignoliellini have been available to me. The presence of clypeal horns in males is here listed as a key-character for the genus *Brignoliella*, but a suppression of such a modification is quite possible in some unknown species of this genus. Thus the placing of species without male clypeal horns into other genera has been argued with several other diagnostic characters.

In my opinion, the monophyly of *Brignoliella*

(as it has been delimited here) is the most indisputable among the known genera of Brignoliellini. On the other hand, the mutual relationships between its subgenera and species groups cannot be established according to the known material.

The range of most known species of *Brignoliella* is exceptionally small, and only *B. quadricornis* is actually known from localities more than 50 km apart. A large number of undescribed species of *Brignoliella* is expected to occur in Southeast Asia.

Brignoliella (*Brignoliella*) Shear, 1978

Type-species: *Polyaspis acuminata* Simon, 1899, according to § 21 (a) (ICZN 1964).

Male palpal bulbus subglobular, palpal tibia slightly thickened, conductor absent. Female epigynal pit variable in size, pits of the preanal plate normally central to submarginal, relatively small. Male clypeal horn relatively small, cheliceral modifications various, but usually relatively small.

Known distribution from Himalaya to Luzon and Fiji, but most species are known from the eastern parts of the total range. The known species are grouped here into four species groups, but the groups are not treated in cladistic sequence, because they are not equally known to me, and their final classification has not been possible.

B. acuminata group

Relatively small yellowish to reddish brown species (1.15–1.3 mm). Margin of carapace in both sexes only rugose, due to general structure of the surface, not serrate as in other species of the tribe.

Male clypeal horn bilobate, male cheliceral horn simple, moderate in size, and distally directed inwards and/or upwards. Female epigynal pit large. Femal preanal plate with submedian pits of variable reciprocal distance, but the pits are not submarginal or marginal in relation to either anterior or lateral margin of the preanal plate.

Four known species from Melanesia and Micronesia.

Brignoliella (*B.*) *acuminata* (Simon, 1889). Figs. 2a–g, 87–89, 91, 107, 109 & 120. Table 3.

Polyaspis acuminata Simon, 1889. Ann. Soc. Ent. France (6)8: 245 (♀).

Paculla acuminata, Simon, 1893. Ann. Soc. Ent. France 62: 324.

Brignoliella acuminata, Shear, 1978. Amer. Mus. Novit. 2650: 26.

Holotype ♀ from New Caledonia, Noumea, in MNHN (Paris), examined. Allotype ♂ with 5 ♂,

7 ♀ from New Caledonia, Dumbea, in litter of *Nothofagus* 7.II.1974, PTL, in MZT.

Other records from New Caledonia: Col de Saramea, in litter of dark jungle 7.II.1974, PTL: 7 ♂ 5 ♀; in litter of sparse forest 7.II.1974, PTL: 3 ♀; Mont Koghi, in litter of dry mountain slope with low bush 6.II.1974, PTL: 5 ♂ 2 ♀; Yahoue, fern slope in moist brookside 6.II.1974, PTL: 1 ♀.

Male 1.25–1.3 mm. Clypeus with wide, bilobate horn. Eyes subequal in size and close to each other, but not larger than the average for this tribe. Lower part of carapace coarsely reticulated, thoracic area finely reticulated, sides of cephalic area almost smooth. Chelicerae anteriorly with a blunt basal knob, continued obliquely downwards by a strong carina. This carina terminates in a short, falciform tooth. Viewed dorsally, the apex of this tooth points inwards, but in anterior view the wide tooth is directed obliquely upwards. The cheliceral modifications are totally situated in the upper cheliceral half.

Sternum moderately pitted, pulmonary plate with slightly smaller pits. Abdomen long oval, dorsal scutum distinctly pitted. Lateral scutum I short, continued by a row of small plates.

Male palpal bulbus with totally unmodified femur and patella, tibia slightly swollen. Bulbus subglobular, embolus long, slightly bent and distally tapering.

Female 1.2–1.3 mm. Carapace, chelicerae, and sternum without horns and teeth, but otherwise structurally similar to corresponding parts of the male.

Abdomen short oval to subcircular. Postgenital plate larger than in male, preanal plate with paired pits far both from each other and from the lateral margin. Epigynal pit large, transversely oval, posterior part covered by the folded margin of the pulmonary plate.

B. acuminata is differentiated from males of other species of this group by shape of the clypeal and cheliceral horns, and from corresponding females by different shape and position of the pits of the preanal plate. The details of the female genitalia are slightly different, but the diagnostic value of this character is less significant.

B. acuminata was found in New Caledonia by the author in a variety of moist and dry natural habitats, and it is probably a common species at least in the southern half of New Caledonia.

Brignoliella (*B.*) *vitiensis* sp. n. Fig. 100. Table 3.

Holotype ♀ with one paratype ♀ from Fiji, Viti Levu, Nausori district, Longani, in litter of bush in open, recently cultivated field 3.II.1974, leg. P. T. Lehtinen, in MZT (Turku).

Female 1.25 mm. Submedian pits of the preanal plate of female wide apart, reaching to the anterior margin of the plate. This plate is distinctly shorter than in *B. acuminata*.

Whole carapace more smooth than in *B. acumi-*

nata, granules on the dorsal elevation in a single row along the margin. Sternum pitted, but less densely than in *B. acuminata*. Epigynal orifice relatively wider than in *B. acuminata*.

Brignoliella (B.) *beattyi* Shear, 1978

B. beattyi Shear, 1978. Amer. Mus. Novit. 2650: 27, figs. 68—71.

Holotype ♂ and allotype ♀ from Micronesia, Caroline Islands, Palau Islands Group, Arakabesan Island, litter of a dry tropical forest (120 m) 1.III. 1973, J. A. Beatty & J. W. Berry, in BBM (Honolulu).

Male 1.15 mm, female 1.19 mm. For description, see Shear (1978). *B. beattyi* is differentiated from *B. acuminata* by more elongate palpal bulb, shorter embolus, and different modifications of clypeus and chelicerae in the male, and by different shape and position of the pits in the preanal plate in the female. *B. beattyi* is obviously closest to *B. vitiensis*, but the pits of the preanal plate are further apart in the latter species.

Brignoliella (B.) *dankobiensis* Bourne, 1980

B. dankobiensis Bourne, 1980. Rev. Suisse Zool. 87: 304, fig. 5—8.

Holotype ♂ from Papua New Guinea, New Ireland, Lelet Plateau, entrance to Dankobe sink-hole (1150 m), in soil sample, VII.1979, J. D. Bourne, in MHNG (Geneva), not examined. Description and drawings kindly placed at my disposal by Dr. Bourne.

Male 1.36 mm, described in detail by Bourne (1980).

B. dankobiensis is differentiated from *B. acuminata* and *B. beattyi* by longer clypeal horn, larger and more outwardly directed cheliceral horn, as well as by shorter bulb and relatively thicker embolus.

Brignoliella trifida group

Smaller than representatives of other groups. Male clypeal horn with unpaired number of branches (1 or 3). Male chelicerae with wide, depressed lamina. Female epigyne with oval transverse depression. Female preanal plate with posterolateral pits. Possibly related to *B. carmen* group.

Two species known, from Borneo and New Guinea.

Brignoliella (B.) *trifida* sp. n.

Figs. 90, 92 & 114. Table 3.

Holotype ♂ from Indonesia, Kalimantan Timur, Bulungan district, Tarakan Island, Yuata, wet palm jungle 1.XI.1979, PTL, in MZT (Turku), together with three other species of Tetrablemmidae.

Male 1.09 mm. All eyes subequal in size, median eyes circular. Relative size of eyes as in *B.*

acuminata. Cephalic area of carapace dorsally shiny and smooth, thoracic area finely reticulate, only two posterior radiations with distinct rugosity. Clypeus with a large, distally trilobate horn. Profile of the cephalic area almost parallel, slightly rounded towards both ends. Anterior face of chelicerae with low, depressed, but exceptionally wide lamella. This lamella is not connected with the basal tooth, and there are no extra modifications in the chelicerae as in all species of the sympatric *B. vulgaris* group.

Sternum marginally strongly pitted, but central area smooth. Pits of the pulmonary plate smaller and more densely spaced. Preanal plate narrower than in all species of *B. acuminata* group. Lateral scutum I well-developed only down to pulmonary cover plates, the rest is represented only by a thin, continuous fold of the skin. Dorsal abdominal scutum long oval.

Male palpal bulb fairly small, globular. Embolus very long, flat, widest at one-third from the base, distally tapering, apex slightly bent.

Female unknown.

Brignoliella (B.) *delphina* Deeleman-Reinhold, 1980

Brignoliella delphina Deeleman-Reinhold, 1980. Zool. Meded. 56:79; figs. 28—32.

Holotype ♂ and two ♀ paratypes from Jayapura, West Irian (New Guinea), in litter behind dock V on serpentine, 6.I.1954, (L 17), leg. L. van der Hammen, in RMNH (Leiden), not examined. Other paratypes from river Nubai mentioned by Deeleman-Reinhold (1980).

Male 1.08 mm, female 1.04 mm, both sexes described in detail by Deeleman-Reinhold (1980). Smallest known species of *Brignoliella*. Male differentiated from *B. trifida* as well as from all other species of *Brignoliella* by triangular clypeal horn. Female differentiated from all known species of *Brignoliella* by posterolateral position of the pits in the preanal plate.

Small size, type of cheliceral horn, and shape of male bulb refer to relationship with *B. trifida*. It is not very close to the latter species, and a placement into *B. acuminata* group could be possible, too.

Brignoliella carmen group

Relatively large, dark brown species (1.35—1.5 mm). Margin of carapace distinctly serrate to undulate.

Male clypeal horn bilobate, male cheliceral horn large, sublaterally in position. Female epigynal pit wide, but sometimes quite narrow. Female preanal plate with pits extending to the anterior margin of this plate.

Five known species from Himalaya to the Philippines and Micronesia.

Brignoliella (B.) *carmen* sp. n. Figs. 99, 101, 113 & 121. Table 3.

Holotype ♂, allotype ♀ and additional paratypes (5 ♂ 8 ♀ 2 juv.) from the Philippines, Mindanao, Davao City Province, Baguio district, Carmen (900 m), riverside bush litter, 9—10.XI. 1979, PTL, in MZT (Turku).

Male 1.35—1.45 mm. Clypeus with fairly wide, bilobate horn. Ocular area relatively wider than in *B. vulgaris* group, each pair distinctly separated from each other. ALE slightly larger than PME and PLE, PME circular. The whole carapace very finely reticulate, except two posterior, radiating fields of rugose skin. Margin of carapace very distinctly serrate. Anterior face of chelicerae with a strong, wide hook-shaped apophysis. The apex of this apophysis is directed slightly upwards. There are no other cheliceral modifications, not even the basal knob that is typical of most Tetrablemmidae.

Sternum evenly pitted with pits of moderate size, pulmonary plate with much smaller, but as sparsely spaced pits as those of the sternum. Dorsal abdominal scutum oval, very dark brown, shiny, and sparsely pitted. Preanal plate about twice as wide as the postgenital plate. Lateral scutum I short, continued by a row of small plates. Respiratory covers kidney-shaped.

Male palpal femur and patella unmodified, palpal tibia slightly thickened. Palpal bulb much higher than long. Embolus long, basally wide and shallowly curved, distal half abruptly narrowed.

Female 1.45—1.5 mm. Carapace and chelicerae as in male, but without modifications. Dorsal abdominal scutum relatively slightly wider than in male. Preanal plate with large pits close to the anterior margin, ca. half way between the lateral margin and the middle of the plate.

Female epigynal pit large, transversely oval, but posterior margin almost straight. Marginal fold of pulmonary plate small and short, hardly reaching the margin of epigynal pit. Epigynal pit not surrounded by raised area or fold.

Differentiated from *B. bicornis* by less depressed bulb, structure of embolus, and by more widely spaced pits of the preanal plate in female.

Brignoliella (B.) *bicornis* (Simon, 1893) Fig. 119. Table 3.

Paculla bicornis Simon, 1893. Ann. Soc. Ent. France 62: 324. (♂♀).

P. bicornis Simon, 1894. Hist. Nat. Araign. 1(3): 570, figs. 577—581.

Brignoliella bicornis, Shear, 1978. Amer. Mus. Novit. 2650: 26.

B. bicornis, Deeleman-Reinhold, 1980. Zool. Meded. 56:80, figs. 33—35.

Lectotype ♂ and allotype ♀ designated herein from several syntypes, from the Philippines, Luzon (Rizal Province), Antipolo, E. Simon, in MNHN (Paris), examined. Five different habitats with leaf litter were studied by the author in Antipolo, but

(no tetrablemmid specimens were collected. One male specimen from Quezon National Park was mentioned by Deeleman-Reinhold, (1980).

Other records, both from Luzon: Laguna Province, Famy, Kapatalan, wet palm jungle 15.XI.1979, PTL: 1 subadult ♀; Benguet Province, Tuba, Asin road 6 km SW of Baguio (700 m), subterranean in rock crevices below mud layer, in wet jungle slope by waterfall, 12.XI.1979, PTL: 2 ♀. Judging from general pattern of geographic speciation of *Brignoliella* in South-East Asia it is probable that the material from Benguet Province belongs to different subspecies or semispecies. However, slight differences between the vulvae of single specimens from Antipolo and Tuba do not allow any further conclusions about the taxonomic status of these populations.

Litter and moss of various forested habitats were intensively studied in the vicinity of the single locality in Tuba as well as in a variety of altitudinal zones and vegetation types in Benguet Province without any additional material of Tetrablemmidae. The same is true for numerous localities in southern Luzon, although habitats typical of *Brignoliella* were regularly studied by the author.

Male 1.5 mm (not 2.5 mm as described by Simon, 1893). Large, dark brown species resembling *B. carmen*. Detailed shape of the clypeal horn not compared with that of *B. carmen*. Anterior cheliceral horn stronger than in *B. carmen*.

Male palpal bulb more depressed than in *B. carmen*. Embolus straight, thick, apex with separate thinner part as in *B. carmen* and especially *B. trifida*. Detailed drawings of the male palpus were kindly sent by Dr. Brignoli for comparison, as the type material was studied by myself before collection of any South-East Asian *Brignoliella*.

Female 1.45 mm (description based on material from Tuba). All chitinous parts, but especially the dorsal abdominal scutum, very dark brown. Patellae yellowish brown, other leg segments reddish brown. Carapace with sparsely spaced marginal undulations, corresponding to typical serrate pattern of all *Brignoliellini*.

Eyes relatively large, all touching each other, ALE distinctly largest, PME oval. Profile of cephalic area posteriorly raised, but abruptly declining at the beginning of the thoracic area. Whole surface of carapace shiny, finely reticulate, marginally more coarse.

Sternum completely pitted, but pits relatively small. Dorsal abdominal scutum oval, shiny, hair pits insignificant. Pulmonary plate wide, densely pitted. Postgenital plate relatively long, when compared to that of *B. acuminata* group. Preanal plate also pitted, but pits smaller than in sternum. The furrows of the preanal plate with strongly sclerotized margins, much closer to each other than in *B. carmen*, and anteriorly curving over the margin of the plate proper. Lateral scutum I short, but continued by a row of small plates.

Posterior margin of the pulmonary plate only centrally folded, the insignificant fold extending only over one-third of the width of the margin. Epigynal pit consists only of a narrow, transverse slit, but the anterior margin of this slit is thickened,

raised, and light in colour, when compared to the surrounding parts of the pulmonary plate. Base of the vulval ducts strongly sclerotized, the anterior margin of this sclerotization centrally with a wide notch. This notch or depression is less distinct in the vulva of the allotype, the drawing of which was kindly sent to me by Dr. Brignoli.

B. bicornis is differentiated from *B. carmen* by details of the genital organs and from all other known South-East Asia species of *Brignoliella* by its large size and very dark colouration.

Brignoliella (B.) *quadricornis* (Roewer, 1963)

Paculla quadricornis Roewer, 1963. Insects of Micronesia 3(4): 127, figs. 9 a—d.

Brignoliella quadricornis, Shear, 1978. Amer. Mus. Novit. 2650: 27, figs. 64—67.

Holotype ♂ and allotype ♀ from Micronesia, Caroline Islands, Kusaie, Fuinwuk, IV.1953, Clarke, in NMNH (Washington), not examined.

Male 1.19 mm, female 1.23 mm. Male chelicerae with strong, upwards directed horn. Female preanal plate with large pits in anterolateral corners. Described in detail by Shear (1978).

Male differentiated from *B. carmen* by longer and more slender palpal femur, and by relatively longer and thinner embolus. Female separated from *B. carmen* by large and more laterally situated pits of the preanal plate. Both sexes are also separated from *B. carmen* and *B. bicornis* by much smaller size.

Roewer (1963 b) and Shear (1978) list many localities of *B. quadricornis* from different islands in Caroline and Marshall Islands, Micronesia. If they represent the same taxon, this is the most widespread species of Tetrablemmidae. However, it is probable that they belong to several subspecies or semispecies.

Brignoliella (B.) *martensi* (Brignoli, 1972)

Figs. 98, 100, 102, 112 & 117. Table 3.

Paculla martensi Brignoli, 1972. Senckenb. Biol. 53: 95, figs. 1—7 (♀).

Brignoliella martensi, Shear, 1978. Amer. Mus. Novit. 2650: 29, fig. 76.

Holotype ♀ from Nepal, (Bagmati Province), Katmandu, Mt. Phulchoki (2500—2730 m), in litter of deciduous forest (*Quercus semicarpifolia*), 9.VIII.1970, J. Martens, in SMF (Frankfurt), examined.

Allotype ♂ with additional 2 ♂ 17 ♀ 3 juv. from Mt. Phulchoki (2000—2100 m), in litter of dry, sparse mountain bush of southern slope, 12.V.1979, PTL, in MZT (Turku).

Male 1.58—1.6 mm. Carapace as in *B. carmen*, but all eyes distinctly smaller. Lateral margins heavily serrate. Clypeal horn relatively longer than

in most species of *Brignoliella* s.str., but also relatively wide. Its apex different in all three specimens of the same population: one (Fig. 98) distinctly trilobate, the other with central, widely triangular lobe reduced, and the third quadrilobate.

All eyes distinctly separated from each other. ALE much larger than the subequal PLE & PME, PME circular.

Male chelicerae with a large cavity between the clypeal margin and the characteristic anterior tooth. Basal part of this cavity with small basomedian elevation, but without well-developed knobs or ridges. The anterior cheliceral tooth is fairly long, directed as in *B. carmen*, but basally continued by a long, oblique ridge. This ridge comprises the margin of the above-mentioned cavity.

Sternal pits as in *B. carmen*. Dorsal abdominal scutum long oval, shiny, distinctly pitted. Posterior part of the pulmonary plate relatively long, pitted. Postgenital plate larger and especially wider than in most *Brignoliella* spp. Preanal plate with reduced pits in the anterolateral corners. Lateral scutum I well-developed, reaching at least to the postgenital plate, but continued by a dense, irregular group of small plates, at least one pair of them corresponding to the perigenital plates of Tetrablemmiini (cf. Shear 1978: 8).

Male palpal femur unmodified, patella slightly lengthened, and tibia moderately swollen. Bulbus short pear-shaped. Embolus falciform, basally not widened.

Female 1.7—1.9 mm (not 1.0 mm as measured by Shear, 1978). Described by Brignoli (1972) and Shear (1978). Similar to male, but modifications of clypeus and chelicerae absent. Shape of dorsal abdominal scutum as in male, but fairly variable within a single population. Lateral scutum I slightly shorter than in male, extending to the posterior margin of the pulmonary plate. Postgenital plate narrower than in male, anterior margin of the preanal plate straight. Pits of the preanal plate moderately large, but smaller than in *Ceratoblemma* spp. and situated at the lateral corner of the anterior margin. Posterior margin of the preanal plate much wider than the pitted anterior margin.

Posterior margin of the pulmonary plate with quite a narrow fold. Epigynal pit large, subcircular, surrounded by a wide dark ring.

The population studied is heterogeneous with regard to the shape of male clypeal horn and to the shape of female abdomen. However, it seems to be sufficiently different from *B. besuchetiana* from Meghalaya, the differences being in details of the genital organs as well as in the dimorphic characters of the male.

Brignoliella (B.) *besuchetiana* Bourne, 1980

Brignoliella besuchetiana Bourne, 1980. Rev. Suisse Zool. 87: 306, figs. 5—8.

Holotype ♂, with 1 ♂ and 3 ♀ paratypes from India, Meghalaya, Garo Hills (400 m), "tamisage en forêt, principalement sous des bambous", 3.XI.1978, C. Besuchet & I. Löbl, in MNHG (Geneva), not examined.

Description and drawings kindly placed at my disposal by Dr. Bourne. Very close to *B. martensi* from Nepal; they probably represent semispecies. Male differentiated from *B. martensi* by distinctly bifid clypeal horn, as well as by details of bulbus and embolus. Differences in females hard to describe because of somewhat schematic drawing of the genital organs by Bourne, but differences are only slight.

Brignoliella vulgaris group

Small, reddish brown species (1.1—1.35 mm). Margin of carapace distinctly, but finely serrate.

Male clypeal horn variable in size, but apex bilobate or bifid. Male chelicerae with a strong tooth, homologous to the tooth of other groups of *Brignoliella*, but 1—2 small teeth may also be present below the strong tooth.

Female epigynal pit small, but it may be surrounded by a large, distinctly coloured or structurally different area. Female preanal plate with small or moderate pair of pits in widely different positions, male preanal plates with less distinct pits in the same position. Small sheet web.

Four known species from Celebes and Borneo. Representatives of this group belong to the dominant spider fauna of leaf litter in these islands. All the species are closely related, but there is no variation in diagnostic characters within single populations. Besides, the structurally closest species are not geographically closest. Under these circumstances, these taxa could not be treated as subspecies.

Brignoliella (B.) *vulgaris* sp. n.

Figs. 94, 96, 118 & 122. Table 3.

Holotype ♂, allotype ♀ and 38 ♂ 120 ♀ 43 juv. paratypes from Malaysia, Sabah, Sandakan district, Till Hill, in leaf litter consisting of enormous leaves of the "tanap" tree, 5.XI.1979, PTL, in MZT (Turku); Till Hill, litter of secondary forest 5.XI.1979, PTL: 3 ♂ 20 ♀ 5 juv.; Sandakan, in litter of jungle slope within the town, 6.XI.1979, PTL: 22 ♂ 47 ♀ 23 juv.

Male 1.20—1.35 mm. Cephalic area of carapace dorsally reticulate and with additional transverse rugosity, the rest of surface of the carapace strongly rugose with wrinkled microstructure, except longitudinal smooth fields in clypeus, situated lateral to the clypeal horn. This horn is fairly long, obliquely downwards directed, and distally bifid.

The eyes are relatively much larger than in any species of the *B. acuminata* group, PME being largest, ALE almost equal to them, and PLE distinctly smallest.

The anterior cheliceral face has a basal cavity between the clypeal margin and the anterior cheliceral teeth. The median basal knob is laterally continued to a weak, curved ridge. The cheliceral tooth proper is rather poorly developed, but there

are two additional black denticles along the same longitudinal axis.

The sternal pits are slightly smaller than those of *B. michaeli*, but larger than in any species of the *B. acuminata* group.

Dorsal abdominal scutum short oval, very distinctly pitted. Ventral plates with smaller pits than the sternum. Preanal plate ca. three times wider than the postgenital plate. Lateral scutum I long, extending as far as the anal plate.

Male palpal femur and patella unmodified, tibia slightly swollen. Bulbus subglobular, embolus straight, without any significant modifications.

Female 1.2—1.35 mm. Carapace and especially clypeus much lower than in male, without horn. Lateral parts of clypeus rugose as the surrounding areas. Chelicerae with strong basomedian knob, but without other modifications.

Dorsal abdominal scutum short oval to subcircular. Preanal plate with fairly large pits at anterolateral corners, strongly resembling the pattern in *B. martensi*. Lateral scutum I shorter, than in male, continued by a row of small plates.

The posterior fold of the pulmonary plate extends over the whole length of the posterior margin, but it has no wider central part covering the epigynal pit. This fold more or less bulges backwards centrally. The epigynal pit itself is very small, but it is surrounded by a very distinct thick V-shaped dark area.

For the male *B. vulgaris*, the shape of the clypeal horn is the best diagnostic character in comparison with any other male specimens of *Brignoliella*. The female is differentiated from the superficially similar species of the *B. vulgaris* group by the pattern of pits in the preanal plate, and from females of *B. martensi* and *B. besuchetiana* by much smaller size.

Brignoliella (B.) *maros* sp. n.

Figs. 97, 116 & 125. Table 3.

Holotype ♂, allotype ♀ and 4 juv. from Indonesia, Sulawesi Selatan, Maros district, Pattunung, base of rock wall with leaf litter bordering a brook, 19.X.1979, PTL, in MZT (Turku).

Male 1.15 mm. Dorsal surface of the cephalic area of carapace finely reticulate, surrounded by several irregular rows of pits with hairs. Clypeus with large pits between the ocular area and the short, bipartite horn. Lateral parts of the cephalic area only finely reticulate. Thoracic area with narrow wrinkled stripes radiating from the foveal region, marginal areas more rugose and the margins themselves strongly serrate.

Eyes relatively smaller than in *B. vulgaris*, ALE>PME>PLE. Chelicerae with no well-defined basal cavity on the anterior face. The strong, lateral tooth almost identical to that of *B. vulgaris*, but the basal extra tooth larger. A small, third denticle as in *B. vulgaris*.

Basal segments of the male palpus as in *B. vulgaris*. Bulbus pear-shaped. Embolus proper short

and straight, but base of embolus with an abruptly narrowed extension of the bulbal tip.

Female 1.2 mm. Shape of carapace as in female of *B. vulgaris*, but pattern of surface sculpture as in male of *B. maros*. Basomedian knob of the female chelicerae weakly developed, but small hairy denticles present instead of the extra teeth of the male chelicerae. Preanal plate with pits distinctly separated, but close to the anterolateral corners. Dorsal abdominal scutum long oval.

The posterior margin of the pulmonary plate with thin fold, without any thickening of wider areas. Epigynal pit subcircular, small. Dark area shining through consists of a thin, straight, transversal figure only.

The male is differentiated from other species of *Brignoliella vulgaris* group by the pear-shaped bulbous, and also by smaller size. The female of *B. maros* is most easily differentiated from other species of *Brignoliella* by the characteristic pits in the clypeus, but also by details of the genital area.

Brignoliella (*B.*) *klabati* sp. n.
Figs. 123. Table 3.

Holotype ♀, from Indonesia, Sulawesi Utara, Minahassa, Tonsea district, Gunung Klabat (1000 m), in jungle litter, 21.X.1979, PTL, in MZT (Turku). A probably deformed ♀ of this species from Gunung Klabat (1400 m), in litter of palm jungle, 21.X.1979, PTL.

Female 1.25 mm. Carapace as in female of *B. maros*, except that the dorsal field of cephalic area, surrounded by pits, is very narrow posteriorly. There is only one row of pits, and the clypeus is sparsely pitted only in lateral parts.

The dorsal abdominal scutum is very long, oval and dark brown in colour. The preanal plate is fairly narrow, and the pattern of its pits is closest to that of *B. vulgaris*, but the pits are relatively larger.

The epigynal pit is small circular, as in *B. maros*, but the dark area around it consists of a wide V-figure.

The other specimen is identical with the holotype, except that the pits of the preanal plate are more weakly developed than corresponding structures of the normal females in this group. The epigynal pit is longitudinally oval and the posterior fold of the pulmonary plate is centrally bulging. There is no dark area around the epigynal pit.

The occurrence of reduced pit in the preanal plates of males in both the *B. vulgaris* group and some species of *B. carmen* group shows that the genes responsible for these pits are not in the sex chromosomes, but that these pits are regulated by some other genes. A small mutation in regulating genes may result in females with some male characters. Another example of such disturbances in sexual characters of tetrablemmids is described on p. 64 for *Tetrablemma brignolii*.

By some standards, *B. klabati* could be regarded only as a subspecies of *B. maros*. However, it is quite probable that the ranges of *B. maros* and *B. klabati* do not meet anywhere, as the *B. vulgaris* group is

represented further to the west in peninsular Sulawesi Utara by structurally more deviating *B. massai*. It is also worth mentioning here that numerous litter samples from Central Sulawesi yielded abundant specimens of *Ablemma*, *Tetrablemma* and *Fallablemma*, but no *Brignoliella*.

Brignoliella (*B.*) *massai* sp. n.
Figs. 93, 95, 115 & 124. Table 3.

Holotype ♂, allotype ♀, and 18 ♂ 53 ♀ 29 juv. paratypes from Indonesia, Sulawesi Utara, Gorontalo district, Datahu (600 m) in litter of jungle slope with dense vegetation of large Araceae sp., 24.X.1979, PTL, in MZT (Turku).

Male 1.1—1.15 mm. Cephalic area of the carapace short, its dorsal field reticulate, and surrounded by irregular rows of hairs in distinct pits. Clypeal pits quite few and situated immediately below the eyes. Lateral parts of the cephalic area more rugose than in *B. maros* or *B. klabati* (♀). Clypeal horns separate, short. Eyes subequal in size.

Chelicerae with a distinct basal boss and a strong tooth. The lower extra tooth is very close to the base of the strong main tooth, and the third denticle is much more median as in related species, and not in the same longitudinal axis as the other extra tooth.

Dorsal abdominal scutum short oval or subcircular, relatively much shorter than in other *Brignoliella* spp. from Sulawesi. Posterior part of the pulmonary plate very wide.

Male palpal bulbous oval, but terminally continued by a short pale apex. This apex gradually changes to black embolus without abruptly narrowed point characteristic of *B. maros*.

Female 1.15—1.3 mm. As the female of *B. maros* with the following exceptions. Clypeal pits few. Basomedian cheliceral knob very strongly developed as in *B. vulgaris*. The whole abdomen as well as the dorsal abdominal scutum much shorter, in all specimens more or less globular, and light brown to reddish brown in colour. Preanal plate with obliquely situated long pits much closer to each other than in other females of *B. vulgaris* group.

Epigynal pit very small and insignificant, partly covered by the posterior fold of the pulmonary plate. No dark areas around the epigynal pit.

The male is most easily differentiated from *B. maros* by the shape of embolus and from *B. vulgaris* by the shape of clypeal horn. The female has a pattern of preanal pits that is unique among *Brignoliellini*. Both sexes are also differentiated from other species of *Brignoliella* from Sulawesi by the short abdomen.

Brignoliella (*Ceratoblemma*) subgen. n.

Type-species *Brignoliella* (*Ceratoblemma*) *michaeli* sp. n. from West Malaysia.

Male palpal bulbous pear-shaped, embolus basally very wide, distally tapering, conductor absent. Female

epigynal pit large, preanal plate with very large pair of pits, surrounded by circular, protruding ridges. Male clypeal horn very long, male cheliceral horn subbasal. Sternum with exceptionally large pits. Both known species are large (1.25—1.8 mm).

Two species known, from Malayan peninsula and Ceylon.

There are two additional large, western species of *Brignoliella*, viz. *B. martensi* and *B. besuchetiana*, but their bulbous is fairly similar to that of the more eastern species of *B. carmen* group, their embolus is practically identical with species of *B. carmen* group. When consistent standards of tetrablemmid subgenera are applied to numerous species of *Brignoliella*, it is evident that *Ceratoblemma* is sufficiently different from *Brignoliella* s. str., although its cladistic relationship with other known groups of *Brignoliella* is not exactly known.

Brignoliella (*Ceratoblemma*) *michaeli* sp. n.
Figs. 103—106, 108. Table 3.

Holotype ♂ from Malaysia, Pulau Pinang, Pinang Hill (730 m), in jungle litter, 21.IX.1978, PTL, in MZT (Turku). Allotype ♀ from Malaysia, Johor, Kota Tinggi district, Biological Field Station, in litter of rain forest 31.X.—4.XI.1976, PTL, in MZT (Turku). * Note. This female specimen belongs to a closely related species, according to rich material of *Ceratoblemma*, collected during the printing of this paper.

Male 1.27 mm (with clypeal horn 1.38 mm). Carapace relatively higher than in all species of *Brignoliella* s. str. Cephalic area wide, and posteriorly further widened as in *Borneomma* spp. Cephalic area finely reticulate, thoracic area rugose. Eyes touching each other; ALE>PME>PLE. Clypeal horn very long, distally bifid, and directed obliquely downwards.

Male chelicerae without basal knob, but the upper margin parallel to the clypeal margin is swollen to a transverse ridge. Anterior face with a short but wide triangular tooth close to the base (position different from all spp. of *Brignoliella* s. str.). This tooth is parallel to the vertical axis of the chelicerae, and its apex is directed obliquely upwards.

Sternum completely pitted with very large pits. Dorsal abdominal scutum oval shiny, hair pits very insignificant. Postgenital and preanal plates equally long, the latter relatively wider than in *Brignoliella* s. str. Anterior corners of the preanal plate with weakly developed pits, corresponding in position to those of the female. For explanation of these pits, see p. 40. Lateral scutum I well-developed, extending as far as the preanal plate.

Male palpal femur and patella unmodified, palpal tibia slightly swollen as in most species of *Brignoliella* s. str. Bulbus pear-shaped, embolus basally wide, moderately curved.

Female 1.3 mm. Clypeus and chelicerae without modifications, cephalic area dorsally narrow and with parallel sides. Dorsal abdominal scutum larger than in male, but similar in shape.

Postgenital plate narrower than in male preanal plate with strongly concave anterior margin, caused by the presence of very large anterolateral pits.

Posterior margin of pulmonary plate with long, but narrow fold. A dark, small, blunt tooth on the anterior margin of this fold covers the posterior margin of the transversely oval epigynal pit. This pit is moderately large in size, and surrounded by a thin dark ring, but the surrounding surface of the pulmonary plate is not modified.

The male *B. michaeli* is easily differentiated from all other tetrablemmids by the long clypeal horn and shape of embolus. The female is separated from *B. scrobiculata* as well as from other species of *Brignoliella* by exceptionally large sternal pits as well as by details of the preanal plate and the genital organs.

Brignoliella (*Ceratoblemma*) *scrobiculata* (Simon, 1893)

Paculla scrobiculata Simon, 1893. Ann. Soc. Entomol. France 62: 324.

Brignoliella scrobiculata, Shear, 1978. Amer. Mus. Novit. 2650: 26.

Holotype ♀ from Ceylon (Sri Lanka, Galle District), Cottawa, in MNHN (Paris), examined at an early stage of this revision, without comparison with recent material of *Brignoliellini*. Drawing of vulva kindly sent to me by Dr. Brignoli.

Femal ca. 1.5 mm (not 3.5 mm, as described by Simon, 1893). Description of structural characters presented by Simon (1893). Male unknown.

Epigyne without distinct, large genital pore. Postgenital plate centrally narrow, laterally widened. Preanal plate with large pits at the anterolateral corners of anteriorly strongly narrowed part. Vulval duct basally thick, strongly sclerotized.

B. scrobiculata is differentiated from all western-oriental species of *Brignoliella* by distinctly larger size, and from all other known species of *Brignoliellini* by the anteriorly much narrowed preanal plate. It is listed here in *Ceratoblemma* because of large size, type of preanal plate and vulva, as well as by its known range.

Brignoliella (*Diploblemma*) subgen. n.

Type-species *Brignoliella leletina* Bourne, 1980, from New Ireland.

Male palpal bulbous flattened subglobular, basal segments of male palpus moderately modified. Embolus long and thin, but a thin conductor, entirely separate from embolus also present.

Brignoliella (*Diploblemma*) *leletina* Bourne, 1980

Brignoliella leletina Bourne, 1980. Rev. Suisse Zool. 87: 302, figs. 1—3.

Holotype ♂ from Papua New Guinea, New Ireland, Lelet Plateau, from jungle soil (1100 m), VII. 1979, J. D. Bourne, in MNHG (Geneva), not examined. Description and drawings kindly placed at my disposal by Dr. J. D. Bourne.

Differentiated from all other species of Brignoliellini by the curious male bulbus with two long, parallel, thin processes, embolus and conductor. According to all other characters, it is a typical *Brignoliella*. The other species of pitted Brignoliellini with conductor and pitted sternum, *Borneomma roberti*, has an entirely different type of hooked conductor far from the base of embolus. According to other characters it is certain that these two species have a conductor by convergence only.

Brignoliellini incertae sedis

"*Brignoliella*" *sarawak* Shear, 1978
Fig. 80, Table 3.

Brignoliella sarawak Shear, 1978. Amer. Mus. Novit. 2650: 29, figs. 72–75.

Holotype ♀ from (Malaysian Borneo) Sarawak, Baleh River, 40 miles upstream from Kapit, 25.IV. 1976, W. Sedgwick, in AMNH (New York), examined.

Female 1.36 mm. Described in detail by Shear (1978). Clypeus with numerous pits. Carapace covered with radiating rows of circular lunules, those of the thoracic area without accompanied hairs. Marginal teeth of carapace squarish, not conical as in most Brignoliellini. Sternal pits large, but smaller than in *B. michaeli*.

Epigynal pit long oval transverse depression. Base of vulval duct strongly sclerotized, especially anteriorly. Ducts very thick, only slightly narrower than the receptacula. Shear's (1978) drawing of vulva does not show the sclerotizations, and he has also misinterpreted the shape of receptacula.

The preanal plate itself is very large, but marginally weakly sclerotized. Two very large sublateral pits are surrounded by strongly sclerotized, protruding margins, and the whole anterior part between these pits is strongly raised in relation to the other parts of the preanal plate.

This species does not fit into the present definition and delimitation of *Brignoliella*, *Borneomma*, or *Pahanga*, but its strange apomorphies do not help in placing it cladistically. It most probably represents a genus of its own, but there remains the possibility that it could be included in some of the genera of Brignoliellini by essential broadening of their definitions.

The male of "*B.*" *sarawak* is still unknown, and its characters will be useful in placing of this deviating species.

Ablemmiini, tribus n.

Shear (1978) placed the genus *Ablemma* as the closest relative of *Singaporemma* into his

Brignoliellini and included *A. pugnax* in the genus *Tetrablemma* in his subfamily Tetrablemmiinae s. str. Such conclusions are difficult to understand when the evolution of single characters in these groups is analyzed separately. They provide that the compact eye group of *Ablemma* and *Tetrablemma* (together with all my Tetrablemmiini) is similar by convergence and not a synapomorphy. At the same time, Shear's conclusions provide that the entirely different vulva of *Ablemma* with well developed trifurcate inner vulval plate could be derived from the vulva of *Brignoliella* and related genera (all with simple transverse type of inner vulval plate and different position of genital orifice, etc.).

In my opinion, the large and widely dominant genus *Ablemma* is not closely related either to Brignoliellini or to Tetrablemmiini, but represents a tribe of its own. The monotypic genus *Sulaimania*, known only by male sex, is preliminarily placed into this tribe, although its exact position is better argued first, when the females will be known.

The total range of Ablemmiini extends from Thailand to the Philippine Islands and New Guinea, including twentyone named species in two genera. All of them live in leaf litter or moss in the ground layer of tropical forests, except two related species that have mostly been recorded from caves.

Ablemmiini is characterized by a modified eye group that usually consists of a compact group of six eyes, more or less similar to the compact eye group of six-eyed Tetrablemmiini and *Hexablemma*. One or two pairs of eyes are reduced in some species of Ablemmiini, leading to similar eye pattern as in *Mariblemma* and *Cuangoblemma* in Tetrablemmiini or *Caraimatta* and *Micromatta* in Mattini. As the evolution of other characters does not contradict, I suggest that this compact eye pattern is a synapomorphy for Ablemmiini, Tetrablemmiini, and Mattini.

The male carapace of Ablemmiini usually has distinct modifications in the ocular area, but sometimes also additional, more posterior modifications. The male chelicerae have a simple tooth that is usually distal in position, and the female preanal plate has corresponding posterolateral or posterior pits. A functionally

similar, but topographically different copulatory locking system has developed independently in many, but not all, Brignoliellini. Many species of Ablemmiini have another copulatory locking mechanism between a sternal pit in female and a corresponding dorsal spine in male. This locking system is present in some, obviously not closely related species in both, certainly monophyletic subgenera of *Ablemma*, and less distinctly in a few further species. It cannot be classified as a synapomorphy, but it is naturally an apomorphic pattern and cannot be regarded as a symplesiomorphy of the species in question. Thus it is again an instance of discontinuous appearance of similar apomorphic structures in a group of related, but not strictly monophyletic species.

The sternal surface is reticulate in most Ablemmiini, but centrally smooth in some species. The pulmonary plate may be slightly pitted in many Ablemmiini, and the epigynal fold is always quite distinct. Leg modifications are rare, and if present (*A. kaindi*), are quite insignificant.

The base of embolus is always modified, but a true conductor is lacking in all known males of Ablemmiini. Embolus is more or less perpendicular to the apex of bulbus both in *Ablemma* and in *Sulaimania*, and as such this is a key character for Ablemmiini, although the synapomorphy of this character between these two genera is not certain. The embolus proper is always modified, at least flattened, never thin and simple as in the majority of species in other tribes of Tetrablemmiinae.

The epigynal orifice of most Ablemmiini is large, distinctly removed from the posterior margin of the pulmonary plate and regularly surrounded by inner sclerotizations. The vulval stem is anteriorly fixed to the inner surface of the pulmonary plate, and its broad distal part is folded inwards as an unpaired extension. Soft basal part of vulval ducts originate directly from the lateral corners of the folded vulval stem, i.e., from the lateral margins of the epigynal pit. The central vulval process is totally absent in all known females of Ablemmiini, while the inner vulval plate is always present and large, obtusely or wide triangular. The apex of this plate is fixed to an inner narrow sclerotized ridge of the pulmonary plate with lateral membranes, not seen

in other groups with a trifurcate type of inner vulval plate.

The type of male and female genital organs of Ablemmiini cannot be directly derived from any extant plesiomorphic patterns in Tetrablemmiinae, and the relationship on Ablemmiini suggested here is widely based on the hypothesis concerning the synapomorphy of the compact eye group in this subfamily. The large epigynal pit far from the margin of the pulmonary plate is directly connected to the paired vulval ducts in Ablemmiini, but leads to an unpaired, sclerotized copulatory channel within a separate vulval stem in Brignoliellini. The large epigynal pit in these two groups is therefore indicative of convergence only, although this character was regarded as a synapomorphy for his Brignoliellini, including *Ablemma*, by Shear (1978).

Ablemmiini is here regarded as a sister group of Tetrablemmiini and Mattini together. Thus, for a taxonomist preferring smaller subfamilies of Tetrablemmiidae, three monophyletic groups, Brignoliellini, Ablemmiini, and Tetrablemmiini+Mattini together could be treated as taxa of same rank, even as subfamilies, while the placing of Fallablemmiini into such a classification would be more problematic. If treated as a subfamily according to these standards, it could be monophyletic, but possibly paraphyletic. Naturally, claim for strictly monophyletic (and not paraphyletic) taxa is necessary for any auxiliary taxon as well, but in presence of some uncertain details of the cladistic of this group, the monophyly of at least the main categories, the subfamilies and the genera, is secured, when using the classification presented in this paper.

Ablemma Roewer, 1963

Ablemma Roewer, 1963. Senckenb. Biol. 44: 228, figs. 9–16.

Tetrablemma, Komatsu, 1968. Acta Arachnol. 21: 35, Pl. 3: figs 1–6.

Tetrablemma, Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 79 (in part).

?*Ablemma*, Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 86 (the same species was listed as *Tetrablemma* on p. 82).

Tetrablemma, Shimojana, 1977. Acta Arachnol. 27: 346.

Ablemma, Shear, 1978. Amer. Mus. Novit. 2650: 31.

Tetrablemma, Shear, 1978. Amer. Mus. Novit. 2650: 12 (in part: *T. pugnax* only).

Ablemma, Deeleman-Reinhold, 1980: Zool. Meded. 56:75.

Type-species by original designation and monotypy *Ablemma baso* Roewer, 1963 from Sumatra. The original description of *Ablemma* and its type-species, including all drawings, is quite misleading.

The range of *Ablemma* extends from Thailand to New Guinea, and its twentyone known species are grouped into two well-defined subgenera. By some standards the number of subgeneric taxa could be higher. As the tribe Ablemini includes only a single species outside this genus, most of the information given above for the tribe is equally true of *Ablemma*, including all data from the females.

Minute to small (0.8–1.35 mm) tetrablemmids with male carapace modified at least in the ocular area, but always without clypeal horns. Eyes 6, 4, or 2, in more or less compact group or recurved row of 4 eyes. Male chelicerae with small acute tooth close to the base of fang, in exceptions more centrally. Females with small pits in posterior margin of the preanal plate (absent in one species); these structures are locked together during copulation. Posterior margin of the preanal plate further with a central slightly convex lamellar extension. Postgenital plate well developed, fairly wide. Lateral scutum I posteriorly reduced to a row of small plates, perigenital plates usually present.

Male bulbus very characteristic: embolus terminal, but originates perpendicularly from the tapering end of bulbus. Embolus flattened or more complicated. Female epigynal area with large orifice, surrounded by complicated inner sclerotizations shining through the integument as distinct dark areas. Central vulval process absent, inner vulval plate with basally wide, centrally tapering central branch.

Both sexes differentiated from *Sulaimania* by entirely different pattern of abdominal plates. Males of *Ablemma* differentiated from those of *Sulaimania* also by type of bulbus and embolus as well as by presence of more distinct modifications of the carapace. The above diagnostic characters are valid in comparison with any other tetrablemmine species.

Ablemma (Ablemma) Roewer, 1963

Type-species *Ablemma baso* Roewer, 1963 from Sumatra.

Minute (0.8–1.05), light-coloured species, mostly living in caves or small crevices of the soil. PME totally reduced in all species, PLE much smaller than ALE in most species, totally reduced in the type-species.

Cephalic area of male carapace posteriorly with a long, pointed tooth. This tooth is also present in females, but is shorter. Male chelicerae converging, copulatory locking tooth subapical, not apical as in most species of the subgenus *Bannia*. The corresponding pits in the female preanal plate close to the posterior margin, not in posterolateral corners as in *Bannia*. Female postgenital plate wide, preanal plate post-

eriorly narrowed, trapezoidal. Posterior end of sternum widely obtuse.

Male palpal embolus basally strongly modified.

Epigynal pit usually very large.

Four species from Sumatra to Ryukyu Islands and Micronesia. *Ablemma* s. str. is more apomorphic than the subgenus *Bannia*, and also more specialized in its habitat selection.

Ablemma (Ablemma) baso Roewer, 1963 Figs. 136–142, Table 3.

Ablemma baso Roewer, 1963. Senckenb. Biol. 44: 228, figs 9–16.

A. baso, Shear, 1978. Amer. Mus. Novit. 2650: 32.

Holotype ♂ and allotype ♀ with 1 ♂ 2 ♀ paratypes from (Indonesia) Sumatra (Sumatera Barat), Baso Cave, X. 1913, E. Jacobson, in SMF (Frankfurt), examined.

The original description is erroneous and misleading with regard to most diagnostic characters, including the total size of the spider and number of eyes.

Male 0.9 mm. Carapace with two large, protruding eyes (ALE) close to each other and a long, obliquely upwards pointing process in the posterior part. Chelicerae with a blunt boss subbasally and a pointed tooth subapically on the anterior face. Sternum smooth, posteriorly narrow, rounded.

Male embolus basally thick, distally slightly screwed and bent.

Female 0.9 mm. Carapace with two flat eyes, dorsal field of the cephalic area horizontal, its posterior corner pointed, but not drawn to a process.

Preanal plate rounded trapezoidal, posterior pit submedian in position.

Epigynal pit very large, its margins only slightly sclerotized.

Differentiated from all known Ablemini by presence of only two eyes. Also differentiated from related species by shape of the dorsal posterior process in male and by details of genital organs in both sexes.

Ablemma (Ablemma) sternofoveata sp. n. Figs. 131–132 & 134–135, Table 3.

Holotype ♀ and one paratype ♀ from Malaysia, Sabah, Tawau district, Bal Estate, Tiger Hill (80 m), jungle litter 2.XI.1979, PTL, in MZT (Turku).

Female 0.85 mm. Carapace with four eyes, two large ALE almost touching and much smaller PLE far from each other. The eye group is actually a short, strongly recurved row. Cephalic area posteriorly gradually raised to constitute a pointed angle similar to *A. baso*. Chelicerae with minute subbasal knob corresponding to the basal boss of most tetrablemmid species. Surface of carapace and sternum almost smooth, finely reticulate along margins. A distinct sternal pit in median line close to the anterior margin.

Dorsal abdominal scutum oval to long oval. Posterior part of pulmonary plate almost as long as wide.

Postgenital plate shorter than preanal plate, parallel-sided. Preanal plate transversely long oval, its posterior pits closer to the posterolateral corner than the median line.

Epigynal pit large, transversely oval, anteriorly limited by a thick, dark, transverse sclerotization.

Differentiated from all other *Ablemma* s. str. by presence of sternal pit, and from pitted species of *Bannia* by anterior position of the sternal pit as well as by position of the pits of the preanal plate and details of genital area.

Male unknown, but the presence of sternal pit in female suggests a male with small erect dorsal tooth.

Ablemma (Ablemma) shimojanai (Komatsu, 1968)

Tetrablemma shimojanai Komatsu, 1968. Acta Arachnol. 21: 35, Pl. 3: figs. 1–6 (♂).

?*Ablemma shimojanai*, Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 86 (non 82!).

T. shimojanai, Shimojana, 1977. Acta Arachnol. 27: 346, figs. 2 A–D. (♂♀).

A. shimojanai, Shear, 1978. Amer. Mus. Novit. 2650: 32, figs. 81–88 (♂♀).

Holotype ♂ from Ryukyu Islands, Okinawa, Ishikawa-shi, Inamiji Cave, 28.IX.1965, Matsuei Shimojana, type deposition unknown.

Shimojana (1977) listed numerous additional records from Ryukyu Islands, including females. The female was also described by Shear (1978), according to additional material from Okinawa (AMNH, New York).

Male 1.0 mm. Four weakly developed eyes in almost straight row, ALE larger than PLE. Male carapace with very long, obliquely backwards directed projection. Chelicerae with a central tooth on the anterior face.

Male palpal bulbus long pear-shaped. Embolus short, strongly screwed.

Female 1.0–1.05 mm. Carapace relatively longer than in male, without long projection. Eye row more recurved than in male according to fig. 83 (Shear 1978), but the degree of reduction in different specimens of both sexes is evidently variable.

Epigynal pit large, subcircular.

Ablemma (Ablemma) berryi Shear, 1978 Table 3.

Ablemma berryi Shear, 1978. Amer. Mus. Novit. 2650: 34, figs. 90–95.

Holotype ♂ and allotype ♀ from Micronesia, Caroline Islands, Palau Island group, Arakabesan Island, litter of mixed tropical forest, 22.II.1973, J. W. Berry, in AMNH (New York), examined.

Male 0.89 mm, carapace posteriorly with an erect process, much shorter than in *A. baso* and *A. shimojanai*. Four eyes in strongly recurved row, ALE larger

than PLE. Chelicerae with short tooth subapically on the anterior face.

Male palpal bulbus pear-shaped. Embolus very complicated, flattened, distally lobed.

Female 0.94 mm. Carapace and chelicerae unmodified. Epigynal pit large, transversely oval.

Preanal plate with submarginal pits in the lateral third.

Differentiated from other pale species of *Ablemma* by erect dorsal process and complicated embolus in male, and by details of epigynal area in female. Also differentiated from *Sulaimania vigelandi* by male cheliceral modification.

Ablemma (Bannia) subgen. n.

Type-species *A. kaindi* sp. n. from New Guinea. Four species of this large subgenus have been recently described by other authors, three by Shear (1978) and Deeleman-Reinhold (1980) in *Ablemma* and one by Brignoli (1973) in *Tetrablemma*. Shear (1978) placed *A. aiya* and *A. sedgwicki* into one species group and the representatives of my *Ablemma* s. str. into the other group.

Minute to small (0.9–1.35 mm) reddish brown or light brown species, all living in litter of forests. Six eyes in compact group, but PME strongly reduced in males or both sexes of some species.

Ocular area variably modified in males, an erect tooth present within or behind the eye group. Cephalic area posteriorly with rounded or obtuse angle or with minute denticle, but never drawn to a pointing process as in *Ablemma* s. str. Female carapace raised in posterior part of the cephalic area. Male chelicerae with a distal tooth at the base of the fang, except in *A. datahu*. This tooth fits into paired pits on the posterolateral corners of the female preanal plate, while the corresponding pits are in other parts of the posterior margin of this plate in *Ablemma* s. str., but also in *A. datahu*. Postgenital plate narrower than in *Ablemma* s. str.

Female sternum with a marked concavity posteriorly, in some species with a central to subdistal pit, depending on the position of the dorsal tooth of the male carapace.

Embolus flattened, but distally simpler than in all known species of *Ablemma* s. str. Vulval sclerotizations more complex than in *Ablemma* s. str.

Sixteen named species from Thailand to New Guinea and the Philippines, especially numerous in Indonesia and surrounding islands. There are several species groups that could be regarded as additional subgenera by some standards. Unfortunately some species are known only by one sex, and thus the creation of an exact cladogram of all the species of *Bannia* is not yet possible. The gap between *Ablemma* s. str. and *Bannia* seems to be very distinct, and structural similarities between single species of them (main locking

mechanism of *Ablemma* type in *A. (A.) datahu* and the locking mechanism of *Bannia* type in *A. (A.) sternofoveata* are fairly simple parallel modifications, not correlated with other diagnostic characters.

Ten species and one subspecies are listed here as *A. kaindi* group, two additional species (*A. erna* & *A. girinumu*) are more distantly related with them, while two species known in both sexes (*A. ruohomaekii* & *A. makiling*) belong to groups of their own. Two species (*A. pugnax* and *A. syahdani*) are known only as females. Their phylogenetic position is somewhat uncertain, but their relations to *A. kaindi* group are expected to be fairly probably.

A. kaindi group

Males of this large group have a pointed tooth in the middle of the ocular area, arising directly from, and including the PME. The females usually have a transverse epigynal pit, limited posteriorly and anteriorly by transverse inner plates, representing the posterior and anterior margins of the vulval stem. The sternal pit is in the posterior concavity of the sternum, occasionally anterior to it.

The species of this group are differentiated from each other mainly by the shape of embolus and profile of carapace in male, and by sclerotization patterns of the epigynal area in females. Distribution from Sumatra to New Guinea.

Five species listed first share the type of male cephalic region. It slopes behind the eye group, while in the rest of species of this group have a more or less horizontal cephalic area. This grouping is made only for identification, and it does not need to imply any accurate relationship.

Ablemma (Bannia) kaindi kaindi sp. n.
Figs. 149, 151, 164, 178, 180, 183 & 191 a,
Table 3.

Holotype ♂, allotype ♀ and 10 ♂, 18 ♀ paratypes from Papua New Guinea, Morobe district, Wau, Mt Kaindi (2850 m), in litter of dense fern stand and in hanging moss of cloud forest, 9.III.1974, PTL, in MZT (Turku); in *Sphagnum* 10.III.1974, PTL: 2 ♂ 1 ♀.

Male 1.2–1.3 mm. Carapace with paired, rounded ridges behind the strongly raised eye group. PME protruding, in profile much higher than in *A. k. avios*. First tibia thickened, except the abruptly narrowed distal part. Distal cheliceral tooth long, acute basal cheliceral boss large. Sternum centrally smooth, marginally reticulate.

Male palpal bulb basally subglobular, but distally

continued by a narrow extension. This bulbal tip is fairly thick, embolus tapers, tip curved outwards.

Female 1.2–1.35 mm. Anterior part of carapace unmodified, but posterior part of the cephalic area raised to a sharper angle than corresponding part of the male. Eye group compact as in all females of *Bannia*. ALE as large as in male, but PLE and PME much smaller.

Epigynal pit transversely oval, with strongly sclerotized margins, and anteriorly limited by a thick transverse figure.

Differentiated from other known species of *A. kaindi* group by large size and in male by presence of rounded ridges behind the ocular area.

The treatment of *A. kaindi* as a single, but geographically variable species is argued primarily by the fact that some of the diagnostic characters within 33 adult specimens of *A. k. kaindi* undergo slight variation. Thus, the exact profile of the male ocular area is not the same in all male specimens, although not identical with that of the single known male specimen of *A. k. avios*. In other species, no variation was found within large populations of at least some of the taxa concerned. Unfortunately, some of the taxa are represented by only single male specimens.

Ablemma (Bannia) kaindi avios ssp. n.
Figs. 150, 166, 179, Table 3.

Holotype ♂ and allotype ♀ from Papua New Guinea, Central district, Mt Albert Edward, Avios (2600 m), in *Sphagnum*, 20.II.1974, PTL, Peter Ivola & John Ingi, in MZT (Turku).

Male 1.25 mm. Eye region less protruding than in *A. k. kaindi*, PME almost horizontal, but their posterior margin drawn to a short tooth. First tibia less distinctly thickened than in *A. k. kaindi*, and basal cheliceral boss smaller.

Palpal bulb distally strongly constricted.

Female 1.25 mm. PME relatively smaller than in *A. k. kaindi*.

Epigynal pit transversely oval, but anteriorly limited by a transverse figure that seems to be centrally constricted. The posterior fold of the pulmonary plate covers only half of the epigynal pit in the single female specimen available, but this may be only a coincidental difference.

Ablemma (Bannia) circumspectans
Deeleman-Reinhold, 1980
Figs. 152, 165 & 181, Table 3.

Ablemma circumspectans Deeleman-Reinhold, 1980.
Zooll. Meded. 56:75, figs 16–22.

Holotype ♂ and 2 ♂ 2 ♀ paratypes from National

Park Kinabalu, Sabah, (Malaysian Borneo), Head Quarters at 1550 m, by sieving leaf-litter of rain-forest, 26–29.VI. 1979, leg. P. R. Deeleman and C. L. Deeleman, in RMNH (Leiden), not examined. Other records from Kinabalu National Park, but also from Tamparuli district listed by Deeleman-Reinhold (1980).

Own material: Malaysia, Sabah, Tuaran district, Mt Kinabalu National Park, Silau Silau trail (1530 m), in litter of rain forest, 10.XI.1976, PTL: 3 ♂ 4 ♀ 1 juv. This is more or less exactly the type locality.

Male 1.15 mm. ocular area raised as in *A. kaindi*, but without paired, rounded ridges. Eyes subequal in size. Clypeus more vertical than in *A. kaindi*, and cephalic area ending posteriorly in a more distinct angle. Carapace and sternum strongly reticulate, sternum centrally with narrow smoother area. Distal cheliceral tooth smaller than in *A. kaindi*, basal knob long, but not protruding.

Male palpal bulb short and wide, pyriform. Embolus flat, centrally widest, distally curved. Embolus is not actually perpendicular in relation to the bulbal tip as in most species of *Bannia*, but obliquely directed outwards.

Female 1.25 mm. Carapace anteriorly unmodified, but cephalic area posteriorly raised. Eyes in compact group, ALE > PLE > PME. Sternum posteriorly strongly concave.

Epigynal pit very low and wide, anteriorly limited by a large complex darkened area.

Differentiated from *A. merotai* and especially from *A. lempake* by larger eyes, and further by details of male profile and genital organs of both sexes. Deeleman-Reinhold (1980) did not know the presence of several semispecies of this group in northern Borneo, and therefore a detailed comparison of the specimens from the Tamparuli district with the type specimens may lead to presence of one more semispecies of this group.

Ablemma (Bannia) merotai sp. n.
Figs. 161, 163 & 173, Table 3.

Holotype ♂ from Malaysia, Sabah, Tawau district, Ranchangan Merotai, in jungle litter, 3.XI.1979, PTL, in MZT (Turku).

Male 1.0 mm. Closely related to *A. circumspectans*, but smaller. All eyes also relatively smaller and ocular area shorter than in *A. circumspectans*. Chelicerae narrower, less divergent, and basal boss weakly developed. Dorsal abdominal scutum shorter oval. Male ocular area higher than in *A. lempake*.

Palpal bulb basally narrower than in *A. circumspectans*, embolus less oblique, relatively narrower and centrally slightly constricted.

Female unknown.

Ablemma (Bannia) lempake sp. n.
Figs. 155, 160, 174 & 188, Table 3.

Holotype ♂, allotype ♀, and 9 ♂ 8 ♀ paratypes from Indonesia, Kalimantan Timur, Kutal district, Lempake, Tanah Merah, in litter of rain forest, 28.I.1979, PTL, in MZT (Turku). Other paratypes: Kutal district, Lao Janan, in litter of partly burnt forest, 30.X.1979, PTL: 10 ♂ 20 ♀; Samarinda district, Samarinda Ulu, Lao Bahu, litter of dense jungle, 27.X.1979, PTL: 1 ♀.

Male 0.9–0.95 mm. Closely related to *A. circumspectans* and *A. merotai*, but no variation of diagnostic characters within the rich material from the Samarinda area. Ocular area lower than in other semispecies of this complex, eyes smaller. Distal cheliceral teeth as in *A. circumspectans* and stronger than in geographically closer *A. merotai*. Basal cheliceral boss very long but low, without an erect anterior projection. Whole sternum coarsely reticulate. First tarsus spindle-shaped.

Palpal bulb basally wider than in *A. merotai*, embolus absolutely perpendicular, long and flat with parallel margins, only tip tapering.

Female 0.9–1.0 mm. All eyes much smaller than in *A. circumspectans*. Preanal plate relatively wider.

Epigynal pit transverse oval, anteriorly limited by light area, and much further anteriorly by a thin, dark arch, representing the margin of the anterior unpaired process of vulval stem, visible far removed from the usual site in this species.

Females easily differentiated from other species of *A. kaindi* group by epigynal area, males by minor details of the embolic division as well as by described non-genital characters.

Ablemma (Bannia) samarinda sp. n.
Figs. 159 & 175, Table 3.

Holotype ♂ and 3 paratype ♂ from Indonesia, Kalimantan Timur, Samarinda district, Samarinda Ulu, Lao Bahu, litter of rain forest, 27.X.1979, PTL, in MZT (Turku).

Male 0.9–0.95 mm. Cephalic area more or less horizontal, ocular area low. Cheliceral tooth very small. Tip of palpal bulb rectangular, without projection opposite the embolus. Embolus short, gradually tapering. Tarsus I slightly swollen.

Female unknown.

The male specimens were found within one hundred meter distance from a single, but quite typical female specimen of *A. lempake*. The shape of male carapace is fairly similar to that of *A. datahu*, *A. sedgwicki*, and *A. raro-sae*, but the male embolic division is much shorter and simple than in any of the mentioned species or any semispecies of the *A. circumspectans* complex. Therefore it is not possible that the female of *A. samarinda*

could be practically identical with that of *A. lempake*. Several species of *Bannia* are found more or less strictly sympatrically also in Lempake (*A. lempake* & *A. syahdani*) and in Mt Makiling, Luzon (*A. makiling* and *A. rarosae*).

Ablemma (Bannia) sedgwicki Shear, 1978
Table 3.

Ablemma sedgwicki Shear, 1978. Amer. Mus. Novit. 2650: 36, figs. 103—107.

Holotype ♂ from (Malaysian Borneo) Sarawak, Baleh River, 40 miles upstream from Kapit, 25.VI.1976, W. Sedgwick, in AMNH (New York), examined.

Male 0.88 mm. Cephalic area horizontal, slightly convex, ocular group not elevated, its central spine obliquely directed.

Palpal bulb with a subcentral constriction as in most preceding species. Tip of bulb bent backwards, embolus narrow, distally curved. Described in detail by Shear (1978).

Female unknown.

Differentiated from other species of *A. kaindi* group mainly by shape of the embolic division, including the characteristic curved apex of bulb.

Ablemma (Bannia) singalang sp. n.
Figs. 157 & 170, Table 3.

Holotype ♂ and paratype ♂ from Indonesia, Sumatera Barat, Padangpanjang district, Gunung Singalang (1750 m), very dark dense jungle with ferns, 25.IX.1978, PTL, in MZT (Turku).

Male 0.92 mm. Carapace similar to that of *A. sedgwicki*, but PME larger, subequal in size to other eyes. Distal cheliceral tooth short and wide. Embolus distally widened, but most resembling that of *A. sedgwicki*. Further differentiated from *A. sedgwicki* by gradually tapering bulb and by thicker base of embolus.

Female unknown.

Ablemma (Bannia) rarosae sp. n.
Figs. 193 & 195, Table 3.

Holotype ♂ from Philippines, Laguna, Calamba, Mt Makiling, NW side at Puting Lupa, 500 m, secondary forest litter, 6.VI.1975, L. A. Corpus Raros, in MZT (Turku).

Male 0.90 mm. Carapace in profile more or less similar to *A. datahu*. A paired knob with hair on clypeus below the eye group. Dorsal field of the cephalic area posteriorly widened in dorsal view, and it is surrounded by distinct setae and a posterior conical tooth. Eyes small, ALE and PLE subequal, PME smaller, but well detectable in spite of the curved tooth in the

central area of the eye group. Chelicerae short and wide, their distal tooth short and wide in comparison with most species of *A. kaindi* group. Subbasal median knob distinct, conical.

Carapace reticulate, with slightly wavy margins. Dorsal scutum centrally with large pits, marginally with normal hair pits. Sternum centrally almost smooth, lateral parts reticulate, but hair pits relatively stronger developed than in other species of *Ablemma*, although not comparable to large pits of typical *Brignoliellini*.

Male palpal bulb without constriction, basal angle of embolus without opposite bulging. Embolus long and flat, its distal third slightly bent inwards and narrower than the basal part. Apex of embolus obtuse. Female unknown.

Differentiated from the sympatric *A. makiling* by distinctly smaller size and by totally different modifications of the male carapace. Differentiated from *A. datahu* by presence of distal cheliceral tooth and by shape and length of embolus.

Ablemma (Bannia) datahu sp. n.
Figs. 158, 162, 176, 189 & 190 b, Table 3.

Holotype ♂, allotype ♀, and 15 ♂ 25 ♀ paratypes from Indonesia, Sulawesi Utara, Gorontalo district, Datahu (600 m), jungle slope with Araceae sp., 24.X.1979, PTL, in MZT (Turku).

Male 0.95 mm. Modifications of carapace of the same type as in *A. samarinda* and *A. rarosae*. Eyes well developed, PME smaller than ALE & PLE. Anterior cheliceral tooth not distal and far from the base of fang, almost centrally of the anterior face of chelicerae. Sternum centrally smooth, laterally reticulate.

Male palpus with long, pyriform bulb, embolus flat, distally outwards curved.

Female 0.95—1.0 mm. Non-genital characters fairly similar to *A. lempake* (females of *A. samarinda* & *A. rarosae* not known!). Preanal plate without pits, corresponding to lack of distal cheliceral teeth in male.

Epigynal pit low, transversely oval, posteriorly without dark limiting strip, anterior sclerotized area shorter than in *A. lempake*.

Differentiated from all other species of *Bannia* by position of the cheliceral tooth in male, and by absence of pits in the preanal plate in female. In spite of that, certainly a member of *A. kaindi* group, and more or less related to *A. samarinda* and *A. rarosae*, both of them among the geographically closest species.

Ablemma (Bannia) aiyura Shear, 1978

Holotype ♂ and allotype ♀ from Papua New Guinea (NE part), Aiyura at 1900 m, VI.1962, R. W. Taylor, in MCZ (Cambridge), examined.

Male 1.0 mm. Described in detail by Shear (1978).

Female 1.1 mm. Sternum with a pit, close to the posterior end (not described by Shear).

Separated from other species of *Bannia* by profile of carapace in males, and by presence or position of the sternal pit in females..

Ablemma (Bannia): species outside the
A. kaindi group.

The following six species are here listed as members of the subgenus *Bannia*, but they are not closely related to each other, and most probably not even to the *A. kaindi* group. Except *A. syahdani*, they live in regions, in which the spider fauna of the ground layer of forests is still quite imperfectly known. It is possible that many of them actually represent groups of their own, taxonomically equal to the *A. kaindi* group.

Ablemma (Bannia) girinum sp. n.
Figs. 156 & 169 Table 3.

Holotype ♂ from Papua New Guinea, Central district, Girinum (Owers Corner), in dark jungle slope (250 m), 13.II.—22.III.1974 by pitfall trap, PTL, in MZT (Turku).

Male 0.9 mm. Carapace highest anteriorly at the eye group, slightly sloping backwards. Six large eyes in compact group, and a sharp, erect tooth between them. Clypeus high, densely covered with short, erect hairs. Distal cheliceral tooth weak, straight. Carapace and sternum strongly reticulated. Dorsal abdominal scutum short oval.

Palpal bulb as in other species of *Bannia*, embolus narrow, distally flattened. Female unknown.

Differentiated from all known species of *Ablemma* by the hair pattern of clypeus. Pale yellow colouration and short abdomen are also characteristic for this species. Somewhat related to *A. kaindi* group, but may belong to a New Guinean group of its own.

Ablemma (Bannia) erna sp. n.
Figs. 154, 171—172, 177 & 187, Table 3.

Holotype ♂, allotype ♀, and 22 ♂ 67 ♀ 1 juv. paratypes from Indonesia, Sumatera Utara, District Tapanuli Utara, Aek Natolu (850 m), jungle slope with thick layer of leaf litter, 24.IX.1978, PTL, in MZT (Turku).

Material from Sumatera Utara, Simalungun district, Gunung Simarpalutuk, close to village Bangun Dolok (1500 m), jungle with continuous moss covering,

23.IX.1978, PTL: 18 ♂ 31 ♀ 2 juv.; Bangun Dolok (1450 m), needle litter of pine forest, 23.IX.1978, PTL: 1 ♂ 6 ♀.

Male 1.0—1.1 mm. Ocular area modified much as in *A. kaindi* with a very conspicuous tooth consisting of PME. Cephalic area ending in a sharp angle. Cheliceral base with no real boss, but faint ridges radiating from a slightly swollen subbasal margin. Distal cheliceral tooth very strong, relatively longer than in *A. kaindi* and *A. lempake* complex. Sternum reticulate, but with a small central, almost smooth area. First tibia and tarsus unmodified.

Palpal bulb obtusely triangular. Embolus flat, falciform, centrally with a small tooth. Base of embolus gradually widens, resulting in a hammer-shaped bulb tip as in *A. kaindi avios*. Besides this, a distally obtuse, anterolaterally directed process is present at the bulb tip. This process is unique within the genus *Ablemma*, but it is very close to the embolic base. It is not called conductor here, although this might be due to only a matter of opinion rather than to strictly deviating structure.

Female 1.1—1.2 mm. Ocular area unmodified, ALE and PLE subequal in size, PME much smaller than them and also much smaller than PME of the male.

Epigynal area very complex. Epigynal pit proper weakly defined, but posteriorly limited by a thick pale, U-shaped elevation, and immediately behind it a wider crescent-shaped, pale ridge. Anterior part of the epigynal area consists of two transverse, parallel, dark figures.

Differentiated from all other species of *Ablemma* by the modifications of the bulb tip in males, and by very complex structure of the epigynal area in females. According to nongenital characters may be related to *A. kaindi* group.

Ablemma (Bannia) syahdani sp. n.
Fig. 186, Table 3.

Holotype ♀ from Indonesia, Kalimantan Timur, Kutal district, Lempake, Tanah Merah, in litter of rain forest, 28.X.1979, PTL, in MZT (Turku). Collected together with rich material of *A. lempake*.

Female 0.9 mm. Carapace similar to *A. datahu*, abdomen longer oval. Preanal plate with a pair of pits close to the posterior margin, but some distance from the posterolateral corners, almost as in all species of *Ablemma* s. str. Posterior corner of sternum with very distinct pit. Surface of sternum completely reticulate.

Epigynal area with two transverse dark bars close to each other. Vulval ducts narrow, straight in basal part.

Male unknown.

Differentiated from all other species of *Bannia* by structure of the preanal plate and

by details of vulva. *A. samarinda* is known from the same area and similar habitat only by males, but the position of cheliceral tooth and the shape and position of dorsal tooth in this species suggest that these structures do not fit into female preanal pits and sternal pit of *A. syahdani*. The distance between type localities of these two species is ca. 25 kilometers. *A. syahdani* may be a relative of *A. datahu*, but in absence of males even its inclusion into *A. kaindi* group remain uncertain.

Ablemma (Bannia) pugnax (Brignoli, 1973)
Fig. 182, Table 3.

Tetrablemma pugnax Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 79, figs. 1—7.

T. pugnax, Shear, 1978. Amer. Mus. Novit. 2650: 12, fig. 21.

Holotype ♀ from Solomon Islands, Guadalcanal, Honiara, 4.VIII.1962, "Noona-Dan Expedition", in ZMC (Copenhagen), examined.

Own material: Papua New Guinea, Milne Bay District, Kiriwina Islands, Losuia, in litter of palm forest with very dense low vegetation close to seashore, 24.II.1974, PTL: 1 ♀.

Female 1.05—1.1 mm. Carapace fairly smooth, except for the marginal areas which are finely reticulate. Dorsal field of the cephalic area with a fringe of pits, each bearing a hair. Cephalic area slightly raised posteriorly, abruptly falling towards the thoracic area. Eye pattern as in most *Bannia*, six eyes, PME smaller than ALE and PLE, ALE largest. Sternum smooth centrally, lateral parts narrowly, but very distinctly reticulate. Dorsal scutum short oval, its posterior margin obtuse. Preanal plate large, posterolateral corners with very distinct pits.

Epigynal fold very wide but short, totally covering the large, transverse oval epigynal orifice. This pit is anteriorly limited by a large, transverse sclerotization.

Male unknown.

Differentiated from other known species of *Ablemma* by the wide epigynal fold and by surface pattern of sternum. Differentiated from all species of *Tetrablemma* by eye pattern, shape and modifications of the ventral plates and by entirely different type of the epigynal area. The drawing of the vulva by Brignoli (1973) is misleading, as stated later by himself (Brignoli 1974). Most probably *A. pugnax* is not closely related with *A. kaindi* group. *A. gtrinum* is a pale New Guinean species of *Bannia* known only by male, but the shape of abdominal plates and sexual

dimorphic characters of carapace and chelicerae as well as much smaller size seem to prove that this male from mountain area of Central district is not conspecific with the female *A. pugnax* from islands of the Solomon Sea. The phylogenetic relationships of *A. pugnax* remain unclear, although it is surely a species of *Bannia*.

Ablemma (Bannia) ruohomaekii sp. n.
Figs. 35, 143—148, 153 & 167, Table 3.

Holotype ♂, allotype ♀, and one paratype ♂ from Thailand, Phetchabun Province, Nam Nao National Park, in litter of bamboo thicket, 19.XI.1976, PTL, in MZT (Turku).

Male 1.0 mm. Carapace with an oval depression immediately behind the eyes, followed by a rounded hump, bearing a small sharp tooth on top. PME of male hardly visible, in female also smaller and darker than the lateral eyes. Chelicerae distinctly divergent, distal tooth strong, obliquely directed outwards. Dorsal scutum long oval.

Male palpal bulbus elongate pyriform, embolus relatively thin, distally curved. Tip of bulbus with rounded triangular projection opposite the embolus.

Female 1.05 mm. Cephalic area dorsally horizontal, posteriorly with an insignificant angle. Sternum with a distinct pit immediately posterior to the centre.

Epigynal pit large circular, anteriorly limited by a thick semicircular inner plate.

Differentiated from all other species of *Bannia* by the position of the dorsal spine, and simultaneously by the whole profile of carapace. Female epigynal area differentiated from *A. makiling* by smaller and less distinctly semicircular anterior dark area.

A. ruohomaekii is both structurally and geographically very distinct from *A. kaindi* group. Some similarities with *A. makiling* probably have no phylogenetic value, and thus *A. ruohomaekii* is an isolated species of *Bannia*.

Ablemma (Bannia) makiling sp. n.
Figs. 187, 191, 192, Table 3.

Holotype ♂ and 3 paratype ♀ from Philippines, Laguna, Mt. Makiling, Makiling Botanical Gardens, 100 m, secondary forest litter, 18.III.1975, L. A. Corpus Raros, in MZT (Turku); 2 ♀ paratypes from Makiling, highest peak, litter from mossy secondary forest, 29.III.1975 L. A. Corpus Raros & R. S. Raros, 1 ♀ in DEUP (Los Baños).

Male 1.03 mm. Sexual dimorphism of carapace resembling the corresponding patterns in *Tetrablemma*, and thus widely different from other species

of *Bannia*. Clypeus long, strongly convex. Ocular group close to the centre of carapace, very distinctly raised from the surrounding surface and centrally with an acute tooth. ALE distinctly larger than PLE, PME not externally distinguishable in the modified central part of the black eye group. Thoracic region behind the eye group with a short practically horizontal area, posteriorly separated from the rest of carapace with a central acute tooth and marginal row of setae.

Basomedian knob very distinct, acute. Distal cheliceral tooth short and wide, but its position is exactly the same as in typical species of *Bannia*.

Sternum completely reticulate. Abdomen long oval. Other non-genital structures as in other species of *Bannia*.

Palpal bulbus gradually tapering towards the apex. Embolus flat and short, apex of embolus obtuse.

Female 1.12 mm. Six eyes constitute an eye group that is similar to other females of *Bannia*. Dorsal area of cephalic region behind the eye group gradually raised and more or less abruptly separated from the thoracic region.

Sternum with a very distinct central pit. Preanal plate slightly wider than long, its posterolateral corners with distinct pits as the majority of species in *Bannia*. Abdomen short oval.

Epigynal area with a dark semicircular anterior part as in *A. ruohomaekii*, but the epigynal orifice is represented only by a narrow slit anterior to a dark transverse fold, posteriorly continued by a large dark area.

Both sexes differentiated from the sympatric *A. rarosae* by distinctly large size. Male differentiated from all known species of *Ablemma* by entirely different type of carapace modifications. Female with characteristic central pit of sternum, further differentiated from *A. ruohomaekii* by details of vulva.

The central position of female sternal pit of *A. makiling* and *A. ruohomaekii* is due to convergence. The corresponding dorsal tooth of male is different in relative position of other carapace modifications between these.

Sulaimania gen. n.

Type-species *S. vigelandi* sp. n. from West Malaysia.

Minute tetrablemmid spiders with four eyes in recurved row. Surface of all sclerotized parts smooth, colouration yellow. Male chelicerae without distal teeth or modifications, male carapace only with a horizontal pointed process in posterior part of the cephalic area, but no modifications in clypeus or ocular area. Postgenital plate exceptionally large, preanal plate relatively small; this is the only tetrablemmid genus with these ventral plates equal in size.

Embolus distal, its base modified.

Female unknown.

Sulaimania vigelandi sp. n.
Figs. 126—130 & 133, Table 3.

Holotype ♂ with 2 paratype ♂ from Malaysia, Johor, Kota Tinggi district, Jalan Lombong, Biological Field Station, in litter of rain forest 31.X.—4.XI.1976, PTL, in MZT (Turku).

Male 0.65 mm, smallest known tetrablemmid species. Carapace dorsally horizontal, cephalic area ending in a short, pointed process, obviously homologous to the posterior horn of *Ablemma* s. str. Anterior eyes much larger than the lateral posterior pair and surrounded by a black area. Clypeus rounded triangular, but without further modifications. Male chelicerae with a blunt central boss on the anterior face, but with no distal or subdistal tooth.

Dorsal abdominal scutum and sternum shining and smooth, sternum posteriorly with rather narrow, rounded apex.

Embolus thin, slightly curved, obliquely originating from the tapering end of pear-shaped bulbus.

Tetrablemmi, tribus n.

Shear (1978) created the subfamily Tetrablemmiinae s. str. for his *Tetrablemma* and several other genera with minute epigynal orifice at the posterior margin of the pulmonary plate. This and other diagnostic characters suggested for differentiation of this group from other Tetrablemmidae seem to be phylogenetically inapplicable. However, there is a natural group of genera, related to the relimited *Tetrablemma*, and a tribe, Tetrablemmi, is suggested for them here. This Tetrablemmi is the largest and most widespread of all tetrablemmid groups. Only *Tetrablemma* and *Cuangoblemma* are included from Shear's (1978) genera, and both of them had to be relimited, leaving also a part of Shear's *Tetrablemma* outside Tetrablemmi.

Rhinoblemma and *Anansia* are new genera based on species known to Shear, while all species of the new genera *Singalangia*, *Shearella*, *Mariblemma*, and *Gunasekara* were unknown to him. At least *Tetrablemma* must be further subdivided into distinct subgenera. These nine genera constitute four different lines of evolution that might be called subtribes, but they are simply listed here as groups of genera, viz. *Shearella-Mariblemma-Gunasekara*, *Tetrablemma-Singalangia-Rhinoblemma*, *Cuangoblemma-Anansia*.

Tetrablemmi is the ecologically most suc-

cessful group of Tetrablemmidae. The majority of species live in litter of natural forests of tropical areas, but many species have adapted to life under bark of trees, and at least one species is found in dry coastal habitats. The above mentioned groups of genera each have a geographically limited distribution, but altogether their range extends over the whole tropical zone of the world.

The number of eyes is six (*Gunasekara* and some *Shearella*) or only two (*Cuangoblemma* and *Anansia*), but four in the large majority of Tetrablemmi. The ocular area of males is more or less modified in all Tetrablemmi, except in *Mariblemma* and in the subgenus *Kumaonia* in *Tetrablemma*. The male chelicerae always have a basally wide anterior horn or tooth. Outside this tribe this kind of cheliceran modification is shared only by *Pahanga dura* in Brignoliellini, where it is certainly a result of convergent evolution. The male cheliceran modifications of Tetrablemmi are not correlated with locking pits in the preanal plate of the females as in Brignoliellini and Ablemmi. The cheliceran modifications of Mattini are quite insignificant and thus the preanal plates of the females in this tribe are also unmodified.

The relative size of the ventral and lateral abdominal scuta is highly variable within Tetrablemmi, but fairly similar between related genera.

The surface of all sclerotized plates is reticulate in the majority of species of Tetrablemmi, but it is secondarily smooth in *Cuangoblemma* (actually very finely granular at magnifications over 500x) and curiously wrinkled in the sternum and carapace of *Gunasekara*. The reticulate structure of sternum is a plesiomorphic character shared by most Tetrablemmi except three genera of Brignoliellini. The well-defined hairs pits of the pulmonary plate of *Shearella*, *Mariblemma*, and *Gunasekara* strongly resemble convergent patterns in Brignoliellini and some Ablemmi.

Minor modifications to male metatarsi or tibiae of the first leg have developed in parallel in some not closely related species of *Tetrablemma* as well as in *Gunasekara*.

The male palpus of Tetrablemmi is usually simple, and as such affords repeated oppor-

tunities for parallel evolution of minor details. No true, separate conductor is ever present in this tribe, but the base of embolus, or in exceptions also more distal parts of the embolus, may be modified in several species of at least *Tetrablemma*.

The type of vulva is characteristic for all species of Tetrablemmi, although almost any part of the complicated plesiomorphic type may be secondarily reduced. The basic type consists of a minute copulatory orifice close to the margin of the pulmonary plate, and a well-sclerotized vulval stem around the copulatory channel. Paired lateral horns of vulval stem normally taper distally, and they usually support the basal parts of the soft vulval ducts. A simple, elongate central process is often present, but reduced in parallel in several evolutionary lines. The inner vulval plate is normally tripartite, and the central branch is then long and slender, not triangular or basally wide as in all Ablemmi and many species of Mattini. This sclerite may also be curiously modified (*Anansia*) or partly reduced (*Shearella* and *Gunasekara*).

Although the typical sexual dimorphism of carapace and chelicerae is quite striking in Tetrablemmi, the most reliable characters for phylogenetic analysis are found in the female genital organs. Therefore samples with mere female specimens can be indisputably placed into correct genera, when the internal genitalia can be cleared or mounted.

The diagnostic characters of Tetrablemmi in comparison with other tribes have been separately discussed in connection with them.

Tetrablemmi is certainly a very old group, and the evolution of many striking characters along several different lines has created a morphologically variable group which can, however, be easily proved monophyletic because of synapomorphy of the type of vulva.

Short diagnosis for the whole tribe: Carapace of males modified, male chelicerae with a basally wide anterior horn. Female preanal plate without distinct pits. Male palpal bulb simple, embolus terminal. Female epigynal orifice small, vulva with pointed lateral horn and usually tripartite inner vulval plate.

The first evolutionary line of Tetrablemmi consists of five large species that live on

islands of the Indian Ocean. They are classified here into three new genera, *Shearella*, *Mariblemma*, and *Gunasekara*.

The only six-eyed Tetrablemmi are found among these species, and their compact eye pattern is similar to that of six-eyed Ablemmi and Mattini. In these genera the male eye group is similar in position to that of the female, but is slightly raised in some species of *Shearella* and very distinctly raised in *Gunasekara*.

The pulmonary plate is strongly pitted, almost as in Brignoliellini, and its anterior margin has a curved row of erect hairs in distinct pits, obviously corresponding to a separate row of small plate each with a single hair in many Brignoliellini. The surface of all sclerotized areas is more rugose than in other genera of Tetrablemmi, and sometimes even wrinkled. The lateral corners of the preanal plate are reticulate, although this surface structure is reduced in most parts of that plate. This reticulate area was erroneously regarded as corresponding to the pits of the preanal plate of *Brignoliella* and *Ablemma* by Brignoli (1978 a).

The first femur of the male is very long and thick in all species of this group and often exceptionally rugose, too.

The male palpus is fairly different in different genera, but the female vulva is characterized by total reduction of the central branch of the inner vulval plate.

Shearella gen. n.

Monoblemma, Shear, 1978. Amer. Mus. Novit. 2650: 23 (in part: *M. browni* only).

Type-species *S. lilawati* sp. n., from Ceylon.

Small (1.2–1.4 mm) tetrablemmid spiders with six or four eyes in compact group in anterior part of carapace of both sexes. Male cheliceran tooth conical, basally wide, but much shorter than in *Tetrablemma*, *Gunasekara*, or *Cuangoblemma*. Abdomen globose, lateral scuta II–IV exceptionally wide.

Male palpal bulb pyriform, embolus simple. Epigynal fold laterally narrow, but centrally wide. Vulva with small central process, inner vulval plate simple transverse.

Shearella lilawati sp. n.

Figs. 2 h–j, 193, 195, 199–200, 205 & 214, Table 3.

Holotype ♂, allotype ♀ and paratypes (55 ♂, 64 ♀, 9 juv.) from Sri Lanka (Ceylon), Batticaloa district, Kalkudah, in litter of scattered bushes on beach and sandy palm forest, 25.I.1969, PTL, M. Saario & H. Hippa, in MZT (Turku).

Male 1.25–1.3 mm. Six eyes in compact group. ALE subequal to PLE, the latter less than one diameter apart. PME less than half a diameter, when compared to the surrounding pairs of eyes. Ocular area more raised than in female, and clypeus more vertical. Carapace with wrinkled or rugose surface, especially along the margins. Male chelicerae with a strong, but short tooth, its apex slightly curved upwards. Sternum relatively wide, slightly convex, laterally reticulated, here and there with small hairs in pits. The pulmonary plate very distinctly pitted. Lateral scutum I with only a short anterior plate. Postgenital plate longer than preanal plate, and relatively longer than in female. Perigenital plates large, usually two on both sides.

Male palpal bulb small, narrowly pear-shaped, ejaculatory duct in two loose coils, distal part almost straight. Embolus basally without abrupt limit to the gradually tapering apex of the bulb.

Female 1.25–1.4 mm. Ocular elevation lower than in male, PLE more than their diameter apart. Chelicerae with a dark median basal carina, and long, but weakly defined basolateral ridge. postgenital plate short, laterally tapering. Prenal plate with rounded margins, anterior margin with a distinct furrow along whole length, but no true pits present. 3–4 unequal pairs of perigenital plates.

Lateral horns of vulval stem long, distinctly curved. Central process quite small, but visible. Copulatory channel narrower than in *S. selvarani*.

Males separated from *S. selvarani* by absolutely and relatively much smaller and narrower bulb. There is no variation in the size and shape of the bulb in the populations of 56 males. Females separated from *S. selvarani* by smaller epigynal pits as well as details of the vulva.

Both sexes separated from *S. browni* by number of eyes.

Shearella selvarani sp. n.

Figs. 201, 207 & 213, Table 3.

Holotype ♂ and allotype ♀ from Sri Lanka (Ceylon), Kandy district, Boopitiya, in litter of moist forest slope, 23.XI.1972, PTL, in MZT (Turku).

Male 1.2 mm. Slightly smaller than *S. lilawati*, but non-genital characters similar to that species.

Male palpal bulb much larger and relatively thicker than in *S. lilawati*. Embolus basally thin.

Female 1.2 mm. Postgenital plate almost as long as the preanal plate, only 2 perigenital plates on each side.

Epigynal fold centrally wide, strongly sclerotized

and black. Epigynal pit visible in the posterior margin of this fold as a transverse pale patch. Lateral horn of the vulval stem almost straight, shorter than in *S. lilawati*. Central process totally reduced, copulatory channel within the vulval stem distinctly wider than in the preceding species.

The distance between type localities of *S. lilawati* and *S. selvarani* is less than one hundred kilometers, but they live in totally different habitats and altitudes. Despite the small morphological differences, they are regarded here as two species.

Shearella browni (Shear, 1978), comb. n.

Monoblemma browni Shear, 1978. Amer. Mus. Nov. vit. 2650: 23 figs. 57—61.

Holotype ♂ from Madagascar, Périnet, III.1969, W. L. Brown, in AMNH (New York), examined. Male 1.33 mm. Described in detail by Shear (1978). Dark reddish brown. Femur I long and strong, slightly curved at both ends, distally thickened, and ventrally rugose.

Female unknown.

This large, four-eyed species is differentiated from *Mariblemma pandani* by rugose carapace, large, pear-shaped bulb, and stronger and longer cheliceral horn. It is differentiated from males of six-eyed *Shearella* spp. by less compact eye group that is not elevated, and by much more coiled ejaculatory duct.

This species shares only a few plesiomorphic characters with *Monoblemma unicum*, externally simple bulb, unmodified embolus, and conical cheliceral horn. However, the cheliceral horn is not similar in profile. The size, surface pattern of carapace, sternum, and pulmonary plate, and dorsal abdominal scutum, profile of carapace, and pattern of abdominal scuta are entirely different in *S. browni* and *M. unicum*.

S. browni is not very close to the two other species of *Shearella*, and it may later be transferred into a genus of its own, but its phylogenetic relationship with other large Tetrablemmi of the islands of Indian Ocean is undisputed. Although sharing the presence of only four eyes with *Mariblemma pandani*, it is not congeneric with this smaller species with thin, fragile legs.

The male tetrablemmid specimen, published as the male of *Hexablemma cataphractum* Berland, 1913 by Simon & Fage (1922) from the Kenyan coast, may be an additional species of *Shearella* or at least of this group of genera.

Its cheliceral process, modification of basal parts of the male bulb and the eye pattern suggest placing into this tribe. Unfortunately, the specimen seems to be lost now. Cf. also p. 74.

Mariblemma gen. n.

Type-species *Paculla pandani* Brignoli, 1978 from the Seychelle Islands.

Eyes four, male ocular group not elevated. Male palpal bulb subglobular, embolus subterminal. Lateral vulval horns very short and thick, central process well developed, but concealed behind the thick bases of vulval ducts.

Mariblemma pandani (Brignoli, 1978), comb. n.
Figs. 202, 204, 206, 208—210 & 216, Table 3.

Paculla pandani Brignoli, 1978. Rev. Zool. Afr. 92: 434, Figs. 1—3 & 5.

Holotype ♂ and 3 ♂ 9 ♀ 1 juv. paratypes from Seychelle Islands, Silhouette, Mare aux Cochons (500 m), under *Pandanus seychellarum*, 3—4.VII.1972, P. L. G. Benoit & J. J. van Mol, in MRAC (Tervuren). 1 ♂ 1 ♀ paratypes with same data in coll. P. Brignoli, examined.

Male 1.05 mm. Eye group in the anterior margin of carapace, eyes subequal in size, PLE separated by 1.5 times their diameter. Apex of the cheliceral tooth bent downwards. Lateral scutum I very short with no posterior plates. Postgenital and preanal plates equally long, one pair of perigenital plates.

Male palpal tibia strongly swollen. Palpal bulb very small, rounded quadrangular, totally filled by the coiled ejaculatory duct. Embolus long and thin, originating subdistally from the inner margin of the distal surface of the bulb.

Female 1.1 mm. Eye group slightly more posterior than in male, due to more sloping clypeus. Chelicerae without modifications. Postgenital plate shorter than in male, three pairs of perigenital plates present.

Epigynal pit distinctly visible, copulatory channel wide. Epigynal fold centrally wider than in *Shearella*. Central vulval process finger-shaped, but not visible in freshly cleared vulva, because ventrally covered with very thick bases of the vulval ducts. When these ducts collapse, the well developed central process becomes visible.

Males differentiated from the four-eyed *Shearella browni* by much smaller and more globular bulb.

It is difficult to understand why Brignoli (1978 a) placed this species into *Paculla*, even with reference to his previous concept of this genus, comprising species listed here in *Brignoliella* and *Afroblemma*. *Mariblemma pandani* is certainly a relative of *Shearella* and as such

its inclusion into Tetrablemmi is undisputed. Even its eye pattern is not far from that of true *Tetrablemma*, and a fairly similar species was described in the same paper as a *Hexablemma*. The concept of *Hexablemma* in Brignoli's earlier paper (1974) clearly is identical with true *Tetrablemma*.

Gunasekara gen. n.

Type-species *G. ramboda* n. sp. from Ceylon.

Large (1.5—1.6 mm) species of Tetrablemmi. Six eyes in compact group in anterior part of the carapace in both sexes. Male chelicerae with strong, distally obtuse horns on the anterior face. Male gnathopodae distally modified, male metatarsi I strongly modified. Sternum exceptionally wide and short. Pulmonary plate strongly pitted. Postgenital, preanal, and perigenital plates similar to *Shearella* spp.

Male palpus with short femur, greatly lengthened and modified tibia. Bulb rounded quadrangular, embolus originates from the inner margin of the apical face. Ejaculatory duct with only one large coil, extending obliquely over the whole length of the bulb. Embolus basally wide, laminar, distally thin.

Epigynal fold centrally very wide, thick, and dark. Lateral horns of vulval stem short, central process absent, inner vulval plate without central branch.

Gunasekara ramboda sp. n.
Figs. 194, 196—198, 203, 211—212, 215, & 217—218, Table 3.

Holotype ♂, alloparatype ♀, and paratypes (12 ♂, 14 ♀, 3 juv.) from Sri Lanka (Ceylon), Nuwara Eliya district, Ramboda Pass (1700 m), in moss under fern trees, I.II.1969, PTL, in MZT (Turku).

Male 1.5—1.55 mm. Clypeus anteriorly pointed, almost triangular as in *Tetrablemma okei*. Clypeus and marginal area of carapace coarsely wrinkled, dorsal part of carapace finely reticulate. ALE>>> PLE>>PME, all situated on erect tubercle. Chelicerae long, anterior horn much longer than in *Shearella* and distally curved backwards. Apex of this horn obtuse, black. Sternum relatively wider than in any other species of Tetrablemmidae, its surface wrinkled and reticulate constituting labyrinthine figure. Metatarsus I with one dorsal, three prolateral and one retrolateral strong tooth.

Palpal bulb with distal boss. There is a concave area between the base of laminar embolus and this boss, limited by a thin ridge.

Female 1.5—1.6 mm. Clypeus more sloping than in the male, eyes on lower elevation. Postgenital plate centrally vertical and thickened at the margin.

Epigynal fold with a protruding central plate. Epigynal pit not externally visible, but the copulatory channel is very wide. Inner vulval plate anteriorly visible as paired obtuse lobes, and there is a central constriction.

G. ramboda is the largest species of Tetrablemmi and among the largest of the whole Tetrablemmi. It is differentiated from all tetrablemmine males by a large number of striking apomorphic characters, and the females also have a very characteristic epigynal fold that is different from all other females of the whole subfamily.

The unreduced number of eyes proves that it has long evolved along different lines from the majority of Tetrablemmi.

A large number of Old World species are more or less related to the type species of the family, and many more are expected to be found in this "subtribe" of Tetrablemmi. According to careful analysis of all characters of this group, the known species are classified into three genera, *Singalanga*, *Tetrablemma*, and *Rhinoblemma*, while the type genus, *Tetrablemma* is easily divided into three morphologically distinct and certainly monophyletic groups that are treated here as subgenera. This is mainly because their total range is large, and in some cases also because of distinct ecological differentiation.

The *Singalanga-Tetrablemma-Rhinoblemma* complex probably lost their PME before differentiation into several taxa, and the type of sexual dimorphism includes a tendency of the male eye group to be transferred into the central or even posterior part of the carapace, while the male cheliceral horn tends to be long and more or less curved backwards. The females share the presence of both the central process and the long and thin central branch of the inner vulval plate. The vulval stem is well sclerotized, and the type of extensions always consists of tapering lateral horns. The epigynal area always bears some kind of furrowed pattern.

Singalanga gen. n.

Type-species *S. sternalis* n. sp. from Sumatra.

Small (1.1 mm) tetrablemmid spiders with four eyes in compact pattern, PLE further apart than in *Tetrablemma*. Patterns of male dimorphic characters unknown. Female cephalic area slightly concave in profile. Carapace, sternum, and pulmonary plate finely reticulate as in *Tetrablemma*. Chelicerae very short, basolateral ridge of female chelicerae insignificant. Sternum posteriorly strongly modified and protruding.

Female abdominal scuta strongly apomorphic: lateral scutum I totally reduced, postgenital plate weakly sclerotized, but strongly modified in shape, preanal plate very wide, anteriorly with paired furrows as in *Pahanga diyaluma* and *P. centenialis* of Brignoliellini.

Epigynal area with a very distinct pattern of deep, transverse furrows. Vulval stem longer than wide, well sclerotized around the copulatory channel, but lateral horns weakly developed.

The only known species of *Singalangia* is the most apomorphic female of known tetrablemmids. Its vulval structure certainly infers relationship with *Tetrablemma*, but the types of vulval modification prove that it is not an apomorphic branch paraphyletically arisen from *Tetrablemma*, but rather a sister group of *Tetrablemma* and *Rhinoblemma* together.

Singalangia sternalis sp. n.
Figs. 225—227, Table 3.

Holotype ♀ from Indonesia, Sumatera Barat, Padangpanjang district, Gunung Singalang, in litter of cloud forest between 1800—2300 m, 27.X.1978, PTL, in MZT (Turku).

Female 1.1 mm. Cephalic area slightly sloping down behind the eye group, but posteriorly ending in an obtuse elevation. Its central hair, typical of all Tetrablemmiini, exceptionally long. ALE >> PLE, ALE oval in shape, placed vertically. PLE circular, more than one diameter apart. Chelicerae short, slightly diverging, both basal modifications insignificant.

Sternum anteriorly wide, posteriorly drawn to a process that is obliquely projected downwards more than the diameter of coxa IV, when viewed laterally. Sternal projection gradually tapering, but distally obtuse. Dorsal abdominal scutum exceptionally long oval. Hair covering of the whole abdomen black.

Posterior part of the pulmonary plate wide quadrangular, anteriorly finely reticulate, but the posterior half completely transversely and deeply furrowed. Postgenital plate weakly sclerotized, but this area is covered by light, hairy skin extending over the whole length of the posterior margin of the pulmonary plate. This light skin is centrally raised, and this swollen central area protrudes at an obtuse angle towards the anterior margin of the preanal plate. The preanal plate has the shape of the upper half of a heart, and there are distinct anterior grooves along the convex parts of the anterior margin. Lateral scutum I is totally absent.

The epigynal fold has paired obtuse extensions on both sides of the epigynal pit. Central process fairly long, fingerlike, central brans of the inner vulval plate long and very thin as in all species of *Tetrablemma*. Vulval stem large, but lateral horns represented only by weakly defined membranes around the base of the ducts of seminal receptacula.

Sternal modifications and furrowed patterns of the epigynal area are also present

in some other species of Tetrablemmiini, but they are not very similar, and do not represent synapomorphic characters with the parallel modifications of *S. sternalis*. The posterior part of the sternum of *Tetrablemma* (*Indonops*) *benoitii* is laterally widened, and thus the sternal modification is paired, while the projection of *S. sternalis* is unpaired. These two species are also differentiated by an entirely different pattern of ventral and lateral abdominal scuta as well as by surface structure of the epigynal area. *T. (Indonops) phulchoki* has a strongly furrowed epigynal area, too, but it has the typical transverse posterior fold, characteristic of all of its relatives, but absent as such in *S. sternalis*. Besides this, the furrows of the epigynal area are more or less semicircular in *T. phulchoki*, but straight in *S. sternalis*. Even in this case, the patterns of abdominal plates are quite different.

Tetrablemma O. Pickard-Cambridge, 1873

Tetrablemma O. Pickard-Cambridge, 1873. Proc. Zool. Soc. London 1873: 114.

Tetrablemma, Butler, 1932. Proc. Roy. Soc. Victoria 44 (N.S.): 111.

Tetrablemma, Roewer, 1963. Insects of Micronesia 3(4):124 (in part).

Tetrablemma, Marples, 1964. Pacif. Sci. 18: 400.

Hexablemma, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 182, not *Hexablemma* Berland, 1920.

Indonops Tikader, 1975. Bull. Brit. Arachnol. Soc. 3: 175. Synonymized with *Tetrablemma* by Brignoli (1976).

Tetrablemma, Shear, 1978. Amer. Mus. Novit. 2650: 8 (in part).

Hexablemma, Brignoli, 1978. Rev. Zool. Afr. 92: 431.

Tetrablemma, Bourne, 1980. Rev. Suisse Zool. 87: 304.

Type-species of *Tetrablemma* by monotypy *T. medioculatum* O. Pickard-Cambridge, 1973, from Sri Lanka. Type-species of *Indonops* by original designation and monotype *I. deccanensis* Tikader, 1975, from India.

Definition and limitation of the type genus of the family Tetrablemmidae has been very vague, and in addition to species belonging to the related *Rhinoblemma*, even species of other tribes (Ablemmiini: *Ablemma*; Mattini: *Hexablemma* and *Caraimatta*) have recently been included in *Tetrablemma* (Blandin 1977, Shear 1978). On the other hand, a close relative of the type-species, *T. rhinoceros*, was recently described in *Hexablemma* (Brignoli 1974).

Minute to small (0.85—1.25 mm) tetrablemmid spi-

ders with four eyes in compact group. Male eye group with a tendency to be set back, even to the posterior half of carapace. Male clypeus more or less convex, sometimes with paired tubercles, but never with unpaired horn (cf. *Rhinoblemma*). Male cheliceral horns long, distally tapering (cf. *Gunasekara*), more or less distinctly directed backwards (cf. *Cuangoblemma* and *Anansia*), but not inwards (cf. *Rhinoblemma*). Female chelicerae with distinct basolateral knob or carina (cf. *Singalangia*). Metatarsi or tibiae of first legs of male sometimes, but not regularly with minor modifications in variable positions.

Postgenital and preanal plates well-developed and unmodified in both sexes, lateral abdominal plate I anteriorly entire, but short, posteriorly represented by a few small plates or only by a fold, perigenital plates usually present.

Surface of sternum, pulmonary plate, and at least lateral parts of carapace reticulate, not pitted.

Male bulbous pear-shaped, embolus terminal, distally simple, but basal or central parts may bear modifications. Ejaculatory duct with thick basal coils (1 1/2—2) and thin, heavily coiled part close to the apex of bulbous.

Female genital area with transverse configurations, varying from faint striae in the cuticle invisible in unmounted specimens to variable pattern of deep furrows. Epigynal pit small, concealed behind the epigynal fold. Vulval stem with distinctly tapering lateral horns supporting the base of vulval ducts posteriorly. Central process more or less fingerlike, always present. Inner vulval plate with a basal transverse part of variable width and a long thin central branch. Seminal receptacula with well defined ducts and saclike receptacula proper.

Tetrablemma is separated from *Singalangia* by largely different pattern of abdominal plates, by well developed lateral horns of vulva, and by lack of apomorphic modifications of the same type in sternum and epigynal area. It is separated from *Rhinoblemma* by different types of sexual dimorphism in the male clypeal area and chelicerae. Unfortunately, detailed information of one sex of both *Singalangia* and *Rhinoblemma* is not available.

The large and very widespread genus *Tetrablemma* is here classified into three subgenera, *Kumaonia*, *Indonops*, and *Tetrablemma* s. str. The first of them, *Kumaonia*, is monotypic as far as known species are concerned. The inclusion of this certainly plesiomorphic species into *Tetrablemma* as suggested by Bourne (1980) makes the definition of the latter more complicated, as the classical pattern of male eyes does not fit to *T. loebli*. However, a careful analysis of all other characters, including the genital organs of both sexes of this species reveals that it is a relative of other Indian species of *Tetrablemma*, and by standards accepted here, also congeneric with them.

All three subgenera have apomorphies of their own, and thus the paraphyly of *Kumao-*

nia and *Indonops* is not probable. On the other hand, *Tetrablemma* s. str. is certainly monophyletic because of several synapomorphies.

The subgenera of *Tetrablemma* are mainly separated on account of distinct synapomorphies of the genital organs of both sexes, but the patterns of non-genital characters of these groups are not in conflict with the cladistics based on the genital characters.

Tetrablemma (*Kumaonia*) subgen. n.

Kumaonia Lehtinen in Bourne, 1980. Rev. Suisse Zool. 87: 316. This citation based on our correspondence brings not *Kumaonia* among available names, because no type-species was definitely selected.

Type-species *Tetrablemma loebli* Bourne, 1980 from western Himalaya.

Eye group of both sexes in anterior part of the carapace. First metatarsus of male with modifications.

Male palpal femur modified in shape, but without distinct swelling or basal, medial process, both typical of *Tetrablemma* s. str. Embolus simple.

Epigynal area with indistinct cuticular striae, but without well-defined furrows, typical of *Indonops* and *Tetrablemma* s. str. Inner vulval plate with very wide basal plate, extending well anterior to the simple central process.

Tetrablemma (*Kumaonia*) *loebli* Bourne, 1980 Figs. 219—224, Table 3.

Tetrablemma loebli Bourne, 1980. Rev. Suisse Zool. 87: 304, figs. 9—16.

Kumaonia simplex Lehtinen in Bourne, 1980. Rev. Suisse Zool. 87: 316. Published in synonymy with *T. loebli*, obviously a technical mistake of Bourne.

Holotype ♂, with 8 ♂ 8 ♀ paratypes from Uttar Pradesh, North India, Kumaon (Bhimtal), 4.X.1979, env. 1500 m.; "lisière d'une forêt secondaire versant est, assez sec; tamisage". Leg. I. Löbl, in MNHG (Geneva), not examined. Additional paratypes from Kumaon district listed by Bourne (1980).

Own material: India, Uttar Pradesh, Kumaon district, Bhimtal (1380 m), in litter of bush close to lake Bhimtal, 7.IV.1979, PTL: 1 ♂ (this specimen, originally selected as the holotype for *K. simplex* was collected in exactly the same locality as the holotype of *T. loebli*!); Kumaon district, Nainital, Pains (1920 m), in litter of stony mountain slope, 16.IV.1979, PTL: 1 ♀; Kumaon district, Takula (1870 m), in open moss covering of sparse mountain bush, 15.IV.1979, PTL: 1 ♀.

Male 0.9 mm. Clypeus rounded, cephalic area horizontal, posteriorly rounded. Eyes relatively small, ALE almost touching, PLE separated from each other by less than their diameter, ALE>PLE. Chelicerae with

long, falciform horns. The base of these horns laterally with a rounded ridge. Dorsal abdominal scutum long oval, very finely chagrined. Postgenital plate longer than in most species of other subgenera. Metatarsus I with a lateral, subdistal conical process which is probably not homologous with metatarsal modifications of other sites in *Tetrablemma* s. str.

Male palpal femur fairly short and basally thick. Bulbus long pyriform, ejaculatory duct with two loose, basal coils. Embolus slightly curved only, fairly long, distally unmodified.

Female 0.95–1.05 mm. Clypeus lower and more sloping than in male. Chelicerae with a well-developed basolateral dark tooth. Legs unmodified. Postgenital plate much shorter than in male.

Epigynal pit small, circular, covered by the epigynal fold. Vulval structure much as in other groups of *Tetrablemma*, except for the wide basal plate of the inner vulval plate, regarded here as a subgeneric character. The drawing of this plate in Fig. 222 is partly misleading, because this wide plate is anteriorly folded.

The male is easily differentiated from all other species of *Tetrablemma* by its plesiomorphic type of carapace, and the female by lack of the strong transverse furrow in the epigynal area, characteristic of all females of *Indonops*, and less distinctly also of all females of *Tetrablemma* s.str. Bourne (1980) tried to compare this species with other Indian species of *Tetrablemma*, but as the majority of the species were unknown to him, the presence of three evolutionary lines in *Tetrablemma* could not be detected by him.

T. loebli is the only known tetrablemmid species that could be expected to occur also within adjacent parts of the Palaearctic region. The locality in Takula much resembles moss-covered habitats of the taiga region, and the same is true for the moss-covered coniferous forest in Darjeeling area, where *Indicoblemma sheari* was recorded by me. Thus tetrablemmids may be later found in typical Palaearctic coniferous forests in Asia.

Tetrablemma (Indonops)

Tikader, 1975, stat. n.

? *Tetrablemma*, Roewer, 1963. Insects of Micronesia 3(4):124 (in part: *T. alterum* only).

Tetrablemma, Marples, 1964. Pacif. Sci. 18: 400. *Hexablemma*, Brignoli, 1974. Publ. cult. Comp. Diam. Angola 88: 841 (in part: *H. viduum* only), not *Hexablemma* Berland, 1913.

Indonops Tikader, 1975. Bull. Brit. Arachnol. Soc. 3: 211.

Tetrablemma, Brignoli, 1976. Bull. Brit. Arachnol. Soc. 3: 211 (*Indonops* = *Tetrablemma*).

Tetrablemma, Benoit, 1977. Ann. Mus. R. Afr. Centr., Sci. Zool. 220: 42.

Hexablemma, Brignoli, 1978. Rev. Zool. afr. 92: 431.

Tetrablemma, Shear, 1978. Amer. Mus. Novit. 2650: 8 (in part).

Type-species by original designation and monotypy *I. deccanensis* from peninsular India.

Eye group of male in central or posterior part of carapace, clypeus marginally rounded, not triangular, in upper part without tubercles. Male chelicerae with fairly simple, distally straight horn as in *Kumaonia*. Male first metatarsi unmodified, tibiae seldom with insignificant ventral modification.

Male palpal femur long and slender, without tubercles or swelling. Bulbus smoothly rounded in profile, embolus without basal modifications. Ejaculatory duct with 1 1/2 coils in basal part of bulbous the main coil oblique. Distal part of ejaculatory duct narrow, slightly coiled only.

Epigynal area in species that are closely related to the type-species without conspicuous furrows, but a strong transverse main furrow and often a complicated pattern of other furrows is present in all species of *T. marawula* group. Fine transverse striae (visible with higher magnifications) present in all species. Vulval stem with lateral horns shining through the integument as a V-shaped figure. Central process of vulva of variable length. Inner vulval plate as in *Tetrablemma* s.str., thus the basal part narrower than in *Kumaonia*.

Although the type-species of *Indonops* is undoubtedly congeneric with the type-species of *Tetrablemma*, a delimited taxon comprising eleven known species is justified, and this subgenus has a wide distribution, from Samoa to St. Helena. In contrast to *Tetrablemma* s. str., the species of *Indonops*, except the type species, usually live in the litter of tropical forests. *Indonops* is both morphologically and ecologically more plesiomorphic than *Tetrablemma* s. str.

Five fairly large species with relatively thick embolus in male and epigynal area without the strong transverse furrow in female are treated here as *T. deccanensis* group.

Tetrablemma (Indonops) deccanensis

(Tikader, 1975)

Figs. 251–252, 262, 272 & 279, Table 3.

Indonops deccanensis Tikader, 1975. Bull. Brit. Arachnol. Soc. 3: 175 figs. 1–8.

Tetrablemma deccanensis, Brignoli, 1976. Bull. Brit. Arachnol. Soc. 3: 211.

T. deccanensis, Shear, 1978. Amer. Mus. Novit. 2650: 9.

Holotype ♀, alloparatype ♂, and several paratypes from India, Maharashtra, Poona, Poona University, under bark of trees, 24.IX.1974, B. K. Tikader, in ZSI (Poona/Calcutta). Material from Poona, Botanical Garden of Fergusson College, 4.VIII.1974, M. S. Malhotra, examined (from private collection of B. K. Tikader — now MZT).

Additional material from Maharashtra listed by Tikader (1975).

Male 1.0 mm. Anterior hump of male carapace short, but longer than in *T. samoensis*. Eyes relatively smaller than in Indian species of *Tetrablemma* s.str., but distinctly larger than in *T. samoensis*. ALE > PLE, PLE separated by slightly less than their diameter. Cheliceral horn shorter than in other Indian species of *Tetrablemma*, slightly curved, but apex straight. Carapace completely reticulate. Dorsal abdominal scutum long oval.

Palpal femur long and slender, unmodified, but palpal tibia strongly swollen, its posterior end globular, projecting backwards. Bulbus very large, almost oval, but distally tapering. Embolus basally wide, distal half spinelike, slightly curved.

Female 1.0–1.05 mm. Carapace with characteristic profile. Cephalic area gradually raised posteriorly, and abruptly sloping down at the margin of thoracic area. Dorsal abdominal scutum long oval. Lateral scutum I consists of a short anterior plate and a fairly long posterior plate, separated by a central part of mere membranous fold. Perigenital plates well-developed, 2–3 pairs. Postgenital plate tightly pressed against the pulmonary plate, laterally narrowed. Preanal plate large, more or less oval.

Epigynal fold narrower than in any other Asian species of *Tetrablemma*. Lateral horn of vulval stem quite narrow, as also seen by the shape of areas shining through the integument. Central process and inner vulval plate as in the majority of *Tetrablemma*.

Separated from *T. samoensis* by yellowish brown colour, profile of carapace in both sexes, as well as by slightly larger eyes. Separated from *T. benoitii* by unmodified sternum, and from representatives of other subgenera in continental Asia by diagnostic characters of the subgenera.

Tetrablemma (Indonops) samoensis

Marples, 1964

Figs. 253–254, 264 & 273, Table 3.

Tetrablemma samoensis Marples, 1964. Pacif. Sci. 18: 400, fig. 1.

T. samoensis, Shear, 1978. Amer. Mus. Novit. 2650: 10 (unjustified emendation).

Lectotype ♂ and alloparatype ♀ designated herein from ♂♀ syntypes from American Samoa, Upolu, Malolololei road, 9.VI.1940, E. C. Zimmermann, in BBM (Honolulu), examined. Not deposited in BMNH (London), as stated by Shear (1978).

Male 1.15 mm. Very dark brown, large. Ocular group central in position, anterior hump very short. Eyes relatively much smaller than in other species of *Tetrablemma*. Cheliceral horn fairly thick and short, almost straight. Carapace and sternum finely

granulated. Lateral scutum I very short, postgenital plate long, perigenital plates absent. Dorsal abdominal scutum wide oval, hairs long.

Palpal bulbus large, embolus very thin, almost straight.

Female 1.2 mm. Very dark brown, large. Carapace in profile rounded, eye group less different in position from that of the male than in other species of *Tetrablemma*. Ventral plates as in male, except that postgenital plate slightly smaller.

Epigynal fold wide, epigynal pit minute, but surrounded by a dark spot.

Separated from all other species of *Tetrablemma* by profile of the carapace in both sexes, but also by very dark colour and large size.

Tetrablemma (Indonops) viduum

(Brignoli, 1974)

Hexablemma viduum Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 184, figs. 16–17.

Tetrablemma viduum, Shear, 1978. Amer. Mus. Novit. 2650: 9.

Holotype ♀ from Angola, Lobito, stony plateau, under a stone, 30.XII.1948, A. de Barros Machado, in MD (Dundo), not examined.

Female 1.2 mm. Description presented by Brignoli (1974). Although no material has been available for study, a comparison of Brignoli's figures with geographically close *T. helenensis* from St Helena proves that these two species are very close to each other, unless synonymous. Other parts of vulva are practically identical, thus the inner vulval plate absent in fig. 16 (Brignoli 1974) has not been observed because of its more dorsal position. I have had difficulties in finding this thin structure in several cases of cleared or mounted tetrablemmid vulvae. The only depicted difference between *T. viduum* and *T. helenensis* seems to be that PLE are distinctly closer to each other in *T. helenensis*. Both of them have a typical vulva of the large species in *Indonops*.

Tetrablemma (Indonops) helenensis

Benoit, 1977

Figs. 267–268, 281, Table 3.

Tetrablemma helenensis Benoit, 1977. Ann. Mus. R. Afr. Centr., Sci. Zool. 220: 42, fig. 16 a-f.

Holotype ♀ from St Helena, Nord, Rupert's Valley, under tussock of *Suaeda fruticosa*, 27.IV.1967, J. Decelle N. & J. Leleup, in MRAC (Tervuren), examined.

Female 1.15 mm. Detailed description presented by Benoit (1977).

The presence of only one tarsal claw in one of the legs studied seems to be due to defective specimen only, and this fact has no phylogenetic significance. The above men-

tioned possible difference in eye pattern could justify specific status for this species which certainly has common origin with the Angolan species. If the dispersal from Angola has occurred long ago, the finished speciation is possible. A possible alternative is, however, that this species has relatively recently dispersed from the nearby African continent with the aid of man or birds. Only comparison of the eye patterns of additional specimens from both areas will finally settle the status of *T. helenensis*.

Tetrablemma (Indonops) benoitii
(Brignoli, 1978) comb. n.
Figs. 228, 261 & 280, Table 3.

Hexablemma benoitii Brignoli, 1978. Rev. Zool. Afr. 92: 431, fig 4.

Holotype ♀ and 2 ♀, 1 juv. paratypes from Seychelle Islands, La Digue (300 m), cut forest, 28–31. VII.1972, P. L. G. Benoit & J. J. van Mol, in MRAC (Tervuren), 1 paratype ♀ coll. P. Brignoli, examined.

Female 0.95 mm. Described by Brignoli (1978). Profile of carapace rounded, eyes subequal in size, PLE less than one diameter apart. Chelicerae short, their basolateral ridge very short. Sternum anteriorly wide, completely reticulate, posterior part modified to a very wide, blunt process that actually has three obtuse angles, the lateral pair being more prominent. Dorsal scutum oval, finely reticulate. Lateral scutum I with short anterior plate only. Postgenital plate short, four pairs of perigenital plates present. Preanal plate as in most species of *Tetrablemma*.

Epigynal fold with strongly convex anterior margin, thus visible part of the pulmonary plate much more concave than in other species of *Tetrablemma*. Epigynal area with numerous convex furrows. Epigynal pit minute, its surroundings not externally dark.

Vulval stem with lateral horns supporting the basal parts of the ducts of seminal receptacula as in all species of *Tetrablemma*. Central process long, distally rounded. Inner vulval plate trifurcate as in all other known species of *Tetrablemma*.

Separated from all other species of *Tetrablemma* by the posterior modified sternum and type of inner vulval plate. Separated from *Singalangia sternalis* by different type of sternal modification as well as entirely different pattern of ventral abdominal scuta and vulval structure. The sternal modifications of these two species are definitely convergent.

T. benoitii is here definitely excluded from *Hexablemma*, and it certainly belongs to *Tetrablemma* s. lat. In absence of males the exact position is somewhat uncertain, but the structure of epigynal area and vulva suggest *Indonops* and not *Tetrablemma* s. str.

Five new species from forest litter from Indonesia to Nepal are treated here as the *T. marawula* group. The palpal bulbus in this group is narrower than in the *T. deccanensis* group, at least in species in which the males are known. The females of the *T. marawula* group are easily placed because of distinct synapomorphy of the epigynal area. There is always a strong, transverse fold, posteriorly limited by deep furrow, parallel to the epigynal fold. The rest of the epigynal area is variously modified in different species.

There is a large variation in size. *T. vietnamensis* is among the largest species of *Tetrablemma*, while *T. marawula* and *T. mardionoi* are the smallest known species of *Tetrablemma*.

Tetrablemma (Indonops) marawula sp. n.
Figs. 255–256, 266 & 281, Table 3.

Holotype ♂, allotype ♀, and 18 ♂ 25 ♀ 15 juv. paratypes from Indonesia, Sulawesi Tengah, Marawula district, Lambara (500 m), riverside jungle litter, 25.X.1979, PTL, in MZT (Turku).

Other material from Sulawesi Tengah: Donggala district, Salena (400 m), litter of bamboo/coconut forest, 25.X.1979, PTL: 2 ♂ 7 ♀; Lasuani, litter of bamboo thicket, 20.X.1979, PTL: 4 ♂ 4 ♀ 1 juv.; Baboia, litter of bamboo forest, 20.X.1979, PTL: 2 ♂ 1 ♀ 1 juv. — Tawaeli district, Toboli road, W of Karupua (300 m), litter of mountain forest, 26.X.1979, PTL: 2 ♂.

Male 0.85–0.95 mm. Eyes small, ALE > PLE, PLE separated by slightly less than one diameter. Carapace completely reticulate, except horizontal area anterior to the eyes that is almost smooth. Cheliceral horn narrow, almost straight, except the extreme tip which is strongly curved. Dorsal abdominal scutum long oval, finely reticulate. First legs unmodified.

Palpal bulbus large, distal part abruptly narrowed at the base of embolus. Embolus thin, straight.

Female 1.0–1.05 mm. Cephalic horizontal, except acute process in posterior part that is higher. Size of eyes as in male, but PLE slightly more than their diameter apart. Lateral scutum I anteriorly short, but posteriorly also represented by a continuous, narrow plate or fold, a few small plates between the anterior and the posterior part. 2–3 pairs of perigenital plates. Preanal plate with fairly distinct lateral depressions.

Epigynal area characterized by central swelling of both the postgenital plate and the epigynal fold. A very distinct transverse furrow anterior to the fold. Surroundings of the minute epigynal pit dark. Central process of vulva shorter than in *T. manggarai*.

Differentiated from *T. mardionoi* and *T. manggarai*

by unmodified first tibiae and distally thick bulbus in male and by distinct depressions of the preanal plate in female. Separated from other, geographically more distant species of this group by small size and by details of genital structure.

One male and one female paratype from Lambara have only three eyes, in both cases one of PLE is lacking.

Tetrablemma (Indonops) mardionoi sp. n.
Figs. 247, 257–258, 274 & 282 b, Table 3.

Holotype ♂, allotype ♀, and 2 ♀ paratypes from Indonesia, Sumatera Barat, Padangpanjang district, Gunung Singalang (1600 m), in litter of mountain slope with high grass and a few trees, 25.IX.1978, PTL, in MZT (Turku).

Other material from Padangpanjang district: Gunung Singalang (1750 m), in moss of tree trunks in dark jungle with ferns, 25.IX.1978, PTL: 2 ♀; Lembah Anai, 4 km SW of Padangpanjang (900 m), in litter of jungle of jungle slope, 26.IX.1978, PTL: 2 ♂ 3 ♀.

Male 0.85–0.9 mm. Anterior hump of the cephalic area protruding, but not with processes. Whole carapace coarsely granulated, except numerous smoother patches, including a wide, transverse one between the anterior hump and the eye group. Abdomen short oval. Lateral scutum I strongly reduced, but perigenital plates present. Cheliceral horn relatively short and distally straight. Tibia I retrolaterally thickened, but without a distinct, subcentral tooth.

Palpal bulbus long, distally narrow, gradually tapering. Embolus thin, straight.

Female 0.9–0.95 mm. Profile of carapace gently raised behind the eye group, and cephalic area ends in a minute tooth, but there is no posterior angle. Chelicerae with strong basomedian boss and very distinct basolateral ridges. Lateral scutum I fairly well developed, pattern as in *T. marawula*. Postgenital plate laterally wider than centrally.

Epigynal fold concave, centrally thin and light. Surroundings of the epigynal pit also light, but vulval ducts shining through the integument as quite narrow, dark stripes.

Differentiated from *T. manggarai* by less modified first tibia and narrower palpal tibia in males, from *T. marawula* by presence of this tibial modification. Females of these three species best differentiated by details of vulva.

T. mardionoi is morphologically quite close to *T. manggarai*. However, various natural habitats in Bali and western Java were thoroughly investigated by the author without any record of this group of *Tetrablemmidae*. Both *T. mardionoi* and *T. manggarai* seem to be common species in forest litter in western Sumatra and Flores, respectively. As

the differences are quite constant, these two taxa are regarded here as true species.

Tetrablemma (Indonops) manggarai sp. n.
Figs. 259–260, 269, 282 a & 285, Table 3.

Holotype ♂, allotype ♀, and 2 ♂, 7 ♀ paratypes from Indonesia, Nusa Tenggara Timur, Flores, Manggarai district, Carap (500 m), litter of bamboo forest, 14.X.1979, PTL, in MZT (Turku).

Additional paratypes from Manggarai district: Carap (520 m), litter of extremely dry fern thicket, 14.X.1979, PTL: 1 ♀; Gunung Ranaka (1300 m), twig litter of sparse mountain forest, 13.X.1979, PTL: 1 ♀; Ruteng, litter of bamboo in brookside within town, 15.X.1979, PTL: 1 ♀.

Male 0.95 mm. Anterior hump of the cephalic area horizontal. Whole carapace reticulate. Cheliceral horn slightly bent. Tibia I thickened, retrolateral side with a distinct, short tooth subcentrally. Male palpal tibia thick.

Female 1.0–1.05 mm. Dorsal abdominal scutum oval to long oval. Postgenital plate centrally widest, distinctly tapering towards both ends. Epigynal area with a strong, transverse furrows as *T. marawula*. Central process of vulva very long.

For differential diagnosis, see *T. mardionoi*.

Tetrablemma (Indonops) vietnamensis sp. n.
Figs. 263, 275 & 284, Table 3.

Holotype ♀ from Vietnam, Bac Thai, Vo Ninh, Dinh Ca (250 m), in litter of spiny thicket between large stones at base of high rock wall, 16.X.1978, PTL, in MZT (Turku).

Female 1.25 mm. Carapace relatively long, cephalic area horizontal, slightly convex in profile, and smoothly rounded towards the thoracic area. Cephalic area almost smooth, thoracic area finely granulated. Eyes as in *T. deccanensis*, except that ALE are ca. 0.5 diameters apart. Chelicerae short and thick basolateral ridge long, but not toothlike as in *T. marawula* and related small species. Sternum reticulate, its posterior part between coxae IV narrow, truncate, not concave as in most species of the *T. marawula* group. Abdomen long oval, dorsal scutum marginally smooth, centrally finely reticulate. Lateral scutum only with short anterior plate and a few sparsely spaced minute plates, but no posterior plate. One minute and one large perigenital plate on each side. Postgenital plate trapezoidal.

Epigynal area with more or less distinct transverse furrows and one very strong fold. Posterior margin of pulmonary fold swollen and projecting backwards centrally. Epigynal pit surrounded by an insignificant darker spot, vulval ducts hardly visible.

Differentiated from most Oriental *Tetrablemma* by large size, from *T. phulchoki* by different pattern of folds in the epigynal area. Males of both of these species are unknown.

Tetrablemma (Indonops) phulchoki sp. n.
Figs. 265 & 282, Table 3.

Holotype ♀ and paratype ♀ from Nepal, Bagmati, Phulchoki (2000 m), dry litter of sparse bush in southern mountain slope, 12.V.1979, PTL, in MZT (Turku).

Female 1.05–1.1 mm. Profile of the cephalic area horizontal as in *T. vietnamensis*, except a small posterior denticle. Eyes as in *T. vietnamensis*. Basolateral ridge of chelicerae distinct, but short. Dorsal abdominal scutum long oval, reticulate. Lateral scutum I with a short anterior plate, but posterior part represented only by a membranous fold. Postgenital plate long, rounded trapezoidal, perigenital plates insignificant.

Epigynal area characterized by numerous semicircular furrows. Posterior fold of the pulmonary plate wide dark and projecting centrally. Anterior margin of the postgenital plate also thickened and darkened. A pale spot around the epigynal pit, and a strong fold limiting the posterior margin of semicircular furrows. Lateral horns of vulval stem and other vulval details similar to *T. vietnamensis*.

Differentiated from all other species of *Tetrablemma* by the strong, semicircular furrows of the epigynal area.

Tetrablemma (?Indonops) alterum
Roewer, 1963

Tetrablemma alterum Roewer, 1963. Insects of Micronesia 3(4): 124 figs. 7 g-k & 8 a.

T. alterum, Shear, 1978. Amer. Mus. Novit. 2650: 10, figs. 8–13.

Lectotype ♂ designated by Shear (1978) from ♂♀ syntypes from South Mariana Islands, Saipan, Sadog Talofoto, 13.II.1945, H. Dybas, in FMNH (Chicago), not examined.

Additional material from Micronesia listed by Roewer (1963b), records from Palau regarded as uncertain by Shear (1978).

Male and female 1.1 mm. Described in detail by Shear (1978), measurements and information of structural details incorrect or inaccurate in original description by Roewer (1963b).

Profile of male carapace, distally straight cheliceral horn, long and slender unmodified palpal femur, shape and size of the palpal bulb as well as concave posterior margin of the female pulmonary plate infer *Indonops*, although the centrally modified embolus is very different from all other known species of *Tetrablemma*.

The vulval structure was not depicted in detail by Shear (1978).

Tetrablemma (Tetrablemma)
O. Pickard-Cambridge, 1873

Tetrablemma O. Pickard-Cambridge, 1873. Proc. Zool. Soc. London 1873, 114 (as a genus).

Hexablemma, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88, 182, not *Hexablemma* Berland, 1920 (in part: *H. rhinoceros* only).

Tetrablemma, Shear, 1978. Amer. Mus. Novit. 2650, 8 (in part).

No subgeneric division of *Tetrablemma* has been suggested before, and also the discussion about infrageneric relationships has been vaguely argued. This is partly due to the fact the female of the type-species was not known previously, and also because the embolus of the type-species is exceptionally unmodified.

All species of *Tetrablemma* s. str. live under bark of trees, while all species in other subgenera live in litter of tropical forests, except *T. (Indonops) deccanensis*, which is also a bark species.

The geographical range of *Tetrablemma* s. str. is more western than that of *Indonops*. Most known species live in India or Africa, and only one deviating species, *T. okei* is known from southeastern Australia. The origin of *T. extorris* is unclear.

Eye group of male in posterior part of the carapace, clypeal area often with paired tubercles. Male cheliceral horns distally sharply curved, clypeus more or less triangular at its anterior margin. First metatarsus of male seldom ventrally modified.

Male palpal femur basally with a sharp medial cone, and a subbasal lateral swelling. Bulbus with more or less undulate profile, because the ejaculatory duct has two very thick transversal coils tightly along the inner surface of the bulb. Distal, narrow part of the ejaculatory duct more strongly coiled than in other subgenera. Embolus often with basal projections, but not in the type-species.

Epigynal area without strong external furrows, but the cuticle is heavily striated transversely as in most species of other subgenera. The vulval structures shine through the integument as two transverse dark areas, centrally connected by narrow dark septum. This is caused by wide, strongly chitinized lateral horns of the vulval stem and by dark central area of epigynal fold and well sclerotized inner vulval plate behind this fold. Central area between the lateral horns with uniting, thinner plate, partly covering the central process. Inner vulval plate with long and thin central branch as in other subgenera.

Tetrablemma s. str. certainly represents the most apomorphic group of *Tetrablemma*.

Tetrablemma (T.) medioculatum medioculatum
O. Pickard-Cambridge, 1873
Figs. 230–231 & 244, Table 3.

Tetrablemma medioculatum, O. Pickard-Cambridge, 1873. Proc. Zool. Soc. London 1873: 114 Pl. XII: figs. 1 a-h (♂).

T. medioculatum, Shear, 1978. Amer. Mus. Novit. 2650: 9.

Holotype ♂ from Ceylon (Sri Lanka, Kandy district), Peradeniya Botanical Garden, 1871, J. H. K. Thwaites, in HDE (Oxford), examined.

Male 1.1 mm. Eyes very large, PLE less than their diameter apart. Anterior hump of carapace with small granules. Cephalic area of carapace smooth, thoracic area heavily granulated. Abdomen short oval, dorsal scutum finely granulated and covered with fine short hairs, not significantly pitted. Sternum almost smooth, posteriorly widely rounded.

Palpal femur subbasally with distinct, rounded thickening. Palpal tibia basally rounded, embolus short, distally with flattened and pointed apex.

Female unknown.

Separated from *T. rhinoceros*, *T. brignolii*, and *T. okei* by unmodified base of embolus, from *T. extorris* by smooth anterior hump of the carapace as well as by shape of bulbus and embolus. The nominate subspecies of *T. medioculatum* is most easily separated from the other subspecies by structure of the anterior hump of carapace. The presence of a cline in this character is improbable, because the geographically nearer populations in Sri Lanka and Kerala deviate from each other more than the populations of Sri Lanka and Bihar deviate from each other. These morphologically distinct populations are treated here as subspecies, although there may be more than one species in this group of allopatric taxa.

Tetrablemma (T.) medioculatum cochinese
ssp. n.
Figs. 233, 235, Table 3.

Holotype ♂ and allotype ♀ from India, Kerala, Ernakulam district, Cochin, in park under bark of *Acacia*, 21.IV.1979, PTL, in MZT (Turku).

Male 1.1 mm. Separated from *T. m. medioculatum* by two large teeth on the anterior hump of carapace, by strongly triangular anterior part of the carapace, and by strongly curved apex of the cheliceral tooth. Embolus thin, slightly curved outwards.

Female 1.1 mm. Cephalic area dorsally almost horizontal, a small acute tooth at the angle between cephalic and thoracic areas. ALE > PLE, PLE separated by more than their diameter from each other. Median margin of chelicerae basally well sclerotized, basolateral knob represented by faint ridge only. Dorsal abdominal scutum long oval. Postgenital plate laterally tapering, preanal plate much longer, laterally rounded.

Epigynal fold narrow, extending throughout the whole margin, and distinctly separated from the pulmonary plate proper by a deep furrow. Surroundings of the epigynal pit heavily darkened, darkened figures from vulval ducts laterally tapering.

Male differentiated from all other males of *Tetrablemma* by the strong clypeal modifications.

Female differentiated from other females of *Tetrablemma* s. str. by details of vulva.

Tetrablemma (T.) medioculatum gangeticum
ssp. n.

Figs. 37, 232, 234, 245 & 277, Table 3.

Holotype ♂, allotype ♀, and 2 ♂, 4 ♀ paratypes from India, Bihar, Patna, Biological Garden, under bark of *Diospyros* sp., 10.V.1979, PTL, in MZT (Turku).

Male 1.05–1.15 mm. Separated from *T. m. medioculatum* by low, but wide paired knobs of the cephalic area. These knobs are much less prominent than the horns of *T. m. cochinese*. The clypeal triangle and unpaired hairy knob behind the ocular area are well-developed as in *T. m. cochinese*. The apex of cheliceral horn is only slightly curved.

Male palpal bulb with a subbasal, anterior boss. Embolus longer than in other subspecies of *T. medioculatum*, thin and moderately curved.

Females not distinguishable from those of *T. m. cochinese*.

Tetrablemma (T.) extorris Shear, 1978

Tetrablemma extorris, Shear, 1978. Amer. Mus. Novit. 2650: 12, figs. 14–17.

Holotype ♂ and two paratype ♂ from Trinidad (?), N. A. Weber, in MCZ (Cambridge), examined.

Male 0.82 mm. A detailed description presented by Shear (1978). This is the smallest species of *Tetrablemma* s. str., easily differentiated from all other species by the thick cheliceral horns, distally drawn to a narrow hook. All specimens of the type material are pale yellow; this colouration may also be diagnostic for this species. Structure of palpal femur shows that *T. extorris* belongs to this subgenus. Together with *T. medioculatum*, it is the only species of this subgenus without modifications at the embolic base.

Tetrablemma (T.) rhinoceros (Brignoli, 1974)
Figs. 242, 243 b, 249 & 271, Table 3.

Hexablemma rhinoceros, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 182, figs. 1–15.
Tetrablemma rhinoceros, Shear, 1978. Amer. Mus. Novit. 2650: 9.

Holotype ♂, allotype ♀, and numerous paratypes from Angola, Salazar, 17.III.1973, A. de Barros Machado, in MD (Dundo). Paratype ♂♀ from Angola (coll. P. Brignoli) examined.

Male 1.0 mm. Detailed description presented by Brignoli (1974), but modification of metatarsus I not mentioned by him. Differentiated from *T. brig-*

nolii by smaller size, relatively smaller eyes, and especially by much shorter basal process of embolus. In profile the raised part of cephalic area including the eyes, is continued behind the eyes in *T. rhinoceros*, but falls abruptly downwards behind the eyes in *T. brignolii*. In male paratype of *T. rhinoceros* examined by the author the embolus is strongly curved, but straight in *T. brignolii*.

Female 1.05 mm. Separated from *T. brignolii* by much shorter abdomen, by relatively much smaller and shorter postgenital plate and by semicircular epigynal pit. Vulval structure close to *T. brignolii*.

Separated from *T. medioculatum* by presence of a process at the embolic base, and in both sexes by much smaller eyes.

Tetrablemma (*T.*) *brignolii* sp. n.
Figs. 236, 239, 246 & 278, Table 3.

Holotype ♂, allotype ♀, and 3 ♀ paratypes from India, Tamil Nadu, Nilgiri district, Marappalam (1100 m), under bark of *Artocarpus heterophyllus*, 24.IV.1979, in MZT (Turku).

Male 1.15 mm. Anterior hump of the cephalic area without further modifications. Eyes very large, ALE > PLE, PLE separated by ca. 0.5 diameter from each other. Cephalic area ends in an acute tooth with hair immediately behind the eyes. Cheliceral horns distally strongly curved backwards. Dorsal abdominal scutum long oval.

Palpal femur modified as in *T. medioculatum*. Palpal bulb short pear-shaped, and with an anterior rounded extension including the first coil of the ejaculatory duct. A distinct constriction visible between the two main coils of the ejaculatory duct as in all species of *T. medioculatum* group except *T. extorris*. Embolus long and straight, spinelike, basally with a long and narrow, simple process.

Female 1.15–1.25 mm. Clypeus sloping, eyes subequal in size, slightly smaller than in male. Cephalic area slightly raised posteriorly, ending in an angle with central, small, erect tooth. Dorsal abdominal scutum long oval.

Epigynal pit consists of a narrow, transverse slit at the margin of the pulmonary plate. Lateral horns of vulval stem distally convex, central process long, fingerlike.

One paratype female is partly intersexual. Its chelicerae have a conical tooth in the in anterior face resembling the male cheliceral modifications in *Shearella* and *Monoblemma*.

For differential diagnosis, see *T. rhinoceros*. *T. brignolii* is the allopatric sister species of Angolan *T. rhinoceros*. The morphological differences suggest specific status for these taxa.

Tetrablemma (*T.*) *okei* Butler, 1932
Figs. 237–238, 240–241, 248 a, 250, 270 & 276, Table 3.

Tetrablemma okei Butler, 1932. Proc. R. Soc. Victoria 44 (N.S.): 111, fig. 2: 1–6. (♀).

T. okei, Shear, 1978. Amer. Mus. Novit. 2650: 10 (possible ♂ mentioned, not described).

New material: Australia, Victoria, Yan Yean, in crevices of bark of *Eucalyptus macrorhyncha*, 26.V.1973: 1 ♀; 16.VI.1973: 1 ♂ 3 ♀ juv. (including allotype ♂); 14.VII.1973: 1 ♂ 3 juv.; 21.VII.1973: 4 ♀; 28.VII.1973: 2 ♂ 2 ♀; 4.VIII.1973: 1 ♂ 2 ♀ 1 juv., all leg. A. A. Calder, now in MZT (Turku), kindly made available for study by Mr. John Blyth, Bundoora, Victoria.

Male 1.2 mm. Clypeus strongly narrowed anteriorly. Anterior hump of the cephalic area without further modifications. ALE slightly larger than PLE, PLE more than their diameter apart. Eyes smaller than in the Indian species of this group. Cheliceral horn almost straight, only the extreme tip curved backwards. Maxillae slightly widened. Dorsal abdominal scutum long oval.

Palpal femur with large swelling subbasally, median face with acute basal process, as in the Indian species. Bulbus with anterior rounded extension, and an acute process close to the embolic base. Embolus long, strongly curved. Embolic base with a wide, distally bifurcate process, corresponding in position to the simple process in *T. rhinoceros* and *T. brignolii*. A small tooth close to the orifice of the ejaculatory duct. Metatarsus I with a central, retrolateral tooth.

Female 1.3 mm. Carapace in profile almost horizontal, without distinct posterior angle. Eyes subequal in size, slightly larger than in male, clypeus sloping, anteriorly obtuse as in other females of *Tetrablemma*. Dorsal abdominal scutum long oval. Postgenital plate long and narrow, 2–3 perigenital plates on each side.

Epigynal pit hardly visible, but surrounded by a dark, transverse spot. Vulval structure shines through the integument as long narrow dark stripes, distally not narrowed.

Differentiated from all more western species of *Tetrablemma* s. str. by strongly narrowed clypeus, and bifurcate embolic process in male, by profile of carapace and details of the epigynal area in female. Differentiated from *T. rhinoceros* by more obtuse metatarsal tooth in leg I of male.

Rhinoblemma gen. n.

Tetrablemma, Roewer, 1963. Insects of Micronesia 3: 126 (in part).

Tetrablemma, Shear, 1978. Amer. Mus. Novit. 2650: 10 (in part).

Type-species *Tetrablemma unicornis* Roewer, 1963 from Micronesia, Caroline Islands.

Minute (0.8–0.95 mm) tetrablemmid spiders with strong sexual dimorphism. Four eyes in compact group, in males on tubercle in the posterior half of the carapace as in *Tetrablemma*. ALE much larger than PLE. Male clypeus with a protruding unpaired process and a sharp angle between this process and the eye group. Male cheliceral horns short, curved

strongly inwards. Male palpal structure not exactly known, because the palpi of the holotype are lost and all the descriptions of minute spiders by Roewer are largely erroneous. The embolus was stated to be strongly curved and thin.

The female vulval structure was described as complex by Shear (1987: fig. 7). This figure is either widely misinterpreted or there is confusion of material. There are no ducts in any group of Tetrablemmidae or probably in any haplogyne family which correspond to the ducts in Shear's drawing. However, the male alone is sufficiently distinct from all species of *Tetrablemma* to justify a generic rank.

Rhinoblemma unicornis (Roewer, 1963)
comb. n.

Tetrablemma unicornis, Roewer, 1963. Insects of Micronesia 3: 126, figs. 7 a–f.

T. unicornis, Shear, 1978 Amer. Mus. Novit. 2650: 10, figs. 4–7.

Holotype ♂ and allotype ♀ from Caroline Islands, Palau, Koror, XI.1947, H. Dybas, in FMNH (Chicago), not examined.

Male 0.77 mm, female 0.94. Detailed description by Shear (1978). For differential diagnosis, see description of the genus *Rhinoblemma*.

Cuangoblemma Brignoli, 1974

Cuangoblemma, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 185 (in part).

Cuangoblemma, Shear, 1978. Amer. Mus. Novit. 2560: 24 (in part).

Type-species by original designation *C. machadoi* Brignoli, 1974 from Angola.

Minute (0.85–0.9 mm), pale, short-legged tetrablemmid spiders with 2 eyes close to each other in anterior part of carapace in both sexes. Male carapace low, with a paired tooth immediately anterior to the eyes (cf. p. 34 for paired clypeal tooth in *Brignoliella*). Male chelicerae with thin and straight anterior teeth similar to *Anansia*. Sternum smooth as also other sclerotized parts, posteriorly not modified.

Postgenital plate long and laterally wide in male, long and very narrow in female.

Palpal femur short and relatively thick. Bulbus elongate oval, embolus short, curved. Female vulva with stem and lateral horns of *Tetrablemma*-type, inner vulval plate trifurcate, but lateral branches curved anteriorly, central process short and insignificant.

Cuangoblemma is herewith reduced to monotypic as far as the known species are concerned. Argumentation for this is discussed under *Anansia*.

Cuangoblemma machadoi Brignoli, 1947
Fig. 291, 293–294, Table 3.

Cuangoblemma machadoi, Brignoli, 1974. Publ.

Cult. Comp. Diam. Angola 88: 185, figs. 19–23 & 25 (?not 26), possibly 18 & 24.

C. machadoi, Shear, 1978. Amer. Mus. Novit. 2650: 24.

Holotype ♂ from Angola, close to Salazar, in litter of coffee plantation, 13.I.1970, B. Reis, in MD (Dundo), not examined. Some of the paratype females from the original series obviously do not belong to this species (Brignoli 1974: fig. 26). Male and female paratypes from Salazar, above the waterfall of river Muembege, in litter of humid forest, 18.III.1973, A. de Barros Machado, in collection of P. Brignoli, examined.

Male 0.85 mm. Described in detail by Brignoli (1974). Carapace low, cephalic area horizontal, thoracic area gradually sloping. ALE separated by one diameter, each of them immediately continued to small clypeal horns. Carapace, sternum, and pulmonary plate smooth, very finely granulate with high magnification.

Chelicerae with thin, parallel teeth, directed anteriorly. Sternum posteriorly obtusely rounded. Abdomen long oval, dorsal abdominal scutum smooth.

Palpal tibia posteriorly rounded, much shorter than bulbus. Bulbus elongate oval, distally smoothly tapering. Embolus short, curved, relatively much smaller than in *Anansia astaroeth*.

Female 0.9 mm. There is much confusion in the original description of Brignoli (1974). The affixed drawing (fig. 26) of the vulva is most probably drawn according to a specimen that is not conspecific with the male holotype, but the external description of the female, including figs. 18 & 24, may refer to a female of *C. machadoi*. The original type series most probably consists of females of two minute tetrablemmids, and the mount of vulva alone was made from the wrong species. The female specimen from the collection of P. Brignoli was carefully compared with a male specimen from the same sample, and according to all characters, it seems to be conspecific with it. The only conflicting details seem to be the presence of weakly reticulate margin of sternum and carapace in the female specimen, while the male is totally smooth.

The above female specimen is regarded here as the allotype, and its most important characters are as follows. The carapace is without processes in the ocular area, and the posterior part of the cephalic area is more abruptly sloping. The postgenital plate is as long as in the male, but very narrow. Similar sexual dimorphism is common in Tetrablemmidae, although not present in *Anansia astaroeth*.

The chelicerae are without anterior modifications. The abdominal scutum is long oval (not subcircular as in Brignoli's fig. 18). Position of metatarsal trichobothrium in leg I ca. 0.3, in male ca. 0.35.

The vulva is entirely different from Brignoli's fig. 26, but also very different from the vulva of *Anansia astaroeth*. The ventral part of vulva, including the vulval stem and lateral horns is reminiscent of that of *Tetrablemma*, although the lateral horns are fairly thin. The seminal receptacula, and especially their ducts are very short; the lateral horns support them ventrally rather than posteriorly.

The inner vulval plate is quite exceptional: the lateral arms are directed anteriorly constituting a semicircular anterior figure, while their lateral margins are almost parallel. The central process is not visible ventrally, but in well-cleared specimens a short, distally tapering, but apically rounded process is seen between the vulval stem and the inner vulval plate. There is a slight possibility that the inner vulval plate of the mounted specimen figured by Brignoli was symmetrically broken, but even in such a case the details of the rest of the vulva do not fit the vulva of the alloparatype described above. Brignoli's drawing could well depict an undescribed small species of *Tetrablemma*. Only investigation of all the original material can solve this problem, but the female depicted by Brignoli (1974: fig. 26) is not named here, as its nongenital characters are not known.

C. machadoi cannot be confused with any known species of Tetrablemmidae, because the modification of the ocular area in male as well as the vulva of female are unique.

Anansia gen. n.

Cuangoblemma, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 187 (in part).

Type-species *Cuangoblemma astaroth* Brignoli, 1974 from Angola.

Only two eyes. Male carapace with an erect horn posterior to the eyes. Male chelicerae with more or less straight anterior horn. Female sternum posteriorly concave.

Male palpal femur short as in *Cuangoblemma*. Palpal bulbus without distal notch, embolus thick, strongly curved. Female epigynal area with complicated vulval structure shining through the integument. Inner vulval plate with unique, branched structure, its central branch much stronger and longer than in *Cuangoblemma*.

Brignoli (1974) included the type-species in *Cuangoblemma* because of short palpal femur and obviously also by straight cheliceral horn of the male. He also mentioned the modified ocular area of both species, but actually the type of modification of the male carapace is quite different between *Anansia* and *Cuangoblemma*. The paired tubercle of *Cuangoblemma* is in front of the eyes and that of *Anansia* behind the eyes.

Concerning the detailed structure of the male bulbus, it is evident that the course of the ejaculatory duct is also different between these two genera, while it seems to be fairly similar within all genera of Tetrablemmidae. The most convincing differences are found in the vulval structure. Brignoli (1974) not

only confused the female of *C. machadoi*, but he also misinterpreted the vulva of *A. astaroth*. However, the true female of *C. machadoi* described here is somewhat related with *Anansia* as the strongly modified basal part of the inner vulval plate in both of these genera may represent a synapomorphy. If so, *Anansia* could be the closest known relative of *Cuangoblemma*.

Finally, the pattern of anterior ends of the lateral scuta is I=IV>II=III in *Anansia*, but IV>I>III>II in *Cuangoblemma*. The African fauna of Tetrablemmidae mostly still waits for description and these genera probably do not long remain monotypic.

Anansia astaroth (Brignoli, 1974) comb. n.
Figs. 288—290, 292 & 296, Table 3.

Cuangoblemma astaroth, Brignoli, 1974. Publ. Cult. Comp. Diam. Angola 88: 187, figs. 27—35.
C. astaroth, Shear, 1978. Amer. Mus. Novit. 2650: 24.

Holotype ♂ from Angola, Cuango, Cafunfo, in litter of gallery forest of Rio Capulumba, 20.IV.1970. A de Barros Machado & Peles, in MD (Dundo). Male and female paratypes from Cuango in coll. P. Brignoli, examined.

Male 0.85 mm. Described in detail by Brignoli (1947). Carapace relatively low, cephalic area with a high, distally forked tubercle behind the two eyes (ALE) and an unpaired acute process at the posterior end. There are no traces of PLE in the specimen available to me, and it is probable that fig. 29 of the original description is a misinterpretation. A procurved pattern of lateral eyes is not known for any spider group. The surface of carapace is laterally reticulate, centrally smooth, but finely granular with large magnifications.

The cheliceral processes are almost parallel, thin and directed anteriorly, not upwards as the typical curved apophysis of *Tetrablemma*.

Sternum is fairly broad, posteriorly concave, and completely reticulate.

Abdomen is subglobular, not elongate oval as in *Cuangoblemma machadoi*. Thus both dorsal abdominal scutum and pulmonary plate are shorter, the former subcircular. Pulmonary plate is anteriorly reticulate, posteriorly almost smooth, hairy, but not pitted. Postgenital plate exceptionally long and laterally wider than centrally. Preanal plate transversally long oval, without modifications. Lateral plates exceptionally wide as in *Shearella*, except plate I that is very short and posteriorly not continued by small plates. Perigenital plates minute, 1—2 pairs on both sides.

Legs short. Tarsi much longer than metatarsi, centrally swollen. Position of trichobothrium on metatarsus I ca. 0.4.

Male palpal femur short and thick, as long as

palpal tibia. The latter does not protrude basally, in contrast to *Cuangoblemma machadoi*. Bulbus long oval, distally gradually tapering, embolus very long, fairly thick, falciform, more or less transverse in position.

Female 0.95 mm. Largely similar to the male, except that the modifications of carapace and chelicerae are absent. The abdomen is very globular (not elongate as in fig. 28 in Brignoli 1974). The post-genital plate is almost similar to that of the male (cf. *C. machadoi*). The posterior margin of sternum is still broader than in male, and strongly concave (cf. *C. machadoi*).

Epigynal fold thin, almost parallel, epigynal pit not externally visible. Vulval stem very wide, anteriorly obtusely triangular. Lateral horns of vulva not continuous with the vulval stem as in most Tetrablemmine, including *Cuangoblemma* and *Tetrablemma*, but originate behind the visible part of the vulval stem and obviously surround the base of the vulval ducts, thus resembling the lateral sclerotizations of the vulva of *Hexablemma cataphractum*. The central process is short and hardly visible in uncleared vulva. The inner vulval plate is very complex. The basal plate is semicircular, and only laterally fixed to the margin of the pulmonary plate. Short, paired anterior branches are present dorsal to the thick ducts, but they do not extend anterior to the ducts as homologous structures in *Cuangoblemma*.

A. astaroth is easily differentiated from *Cuangoblemma machadoi* by the modifications of carapace in male and by entirely different type of vulva in female.

Mattini tribus n.

All Neotropical tetrablemmids with conductor in the male palpal bulbus were included in a single genus, *Matta*, by Shear (1978). A detailed analysis of all Neotropical material available has revealed that both female and male genital organs of different species groups of *Matta* are very dissimilar, and they cannot be included in a single genus according to any standards. Most probably the African genus *Hexablemma* is also related to one of these species groups with bulbal conductor. A monophyly of this "*Matta*" — *Hexablemma* complex is possible, but not certain. The relationship of Neotropical tetrablemmids without palpal conductor (*Monoblemma* sensu Shear and Brignoli) to this new tribe, Mattini, remains unclear. As long as the female of *Monoblemma unicum* is unknown, it is neither possible to settle the limitation of the genus *Monoblemma*. There are Neotropical tetrablemmids outside the classical *Matta* with surprisingly similar, but unfortunately fairly plesiomorphic

type of vulva (Fig. 319). Although the distribution and limitation of Mattini is still imperfectly known, it is evident that this tribe is Neotropical-Ethiopian only, without no close relatives in the Oriental-Australian region.

Mattini is certainly more closely related to Tetrablemmine than to any other tribe of Tetrablemmidae, and thus it must be included in the same subfamily even in the case that my Tetrablemmidae should be regarded to represent more than one groups of subfamilial rank. The exact phyletic relationships between different groups of Tetrablemmine and Mattini are not known, and thus either Tetrablemmine or Mattini may be paraphyletic.

In regard to non-genital characters, the species of Mattini are characterized by only minor modifications of male carapace and chelicerae. The unreduced eye pattern of six or four eyes (*Hexablemma* & *Caraimatta*) is posteriorly more open than in all Tetrablemmine. The two eyes of *Matta* and *Micromatta* are far from each other, and without further evidence it is impossible to decide whether the anterior lateral eyes of a compact eye pattern (shared with Tetrablemmine and Ablemmine) have been secondarily separated or totally reduced. If the latter alternative would be correct, the posterior lateral pair of eyes would be the only remaining pair of eyes in these two genera. This kind of reductional pattern is not yet known in spiders.

The palpal segments and also the shape of bulbus is quite variable between different genera of Mattini, and even a strict homology of the suggested synapomorphy, "the conductor of *Matta*" is somewhat uncertain. The bulbal modifications of the type-species of *Matta*, *M. hambletoni*, consist of a circular complex of ridges around the base of embolus, while some parts of this ring have been strongly enlarged in the other species of true *Matta*, *M. mckenziei*. The bulbal modifications of *Micromatta* and *Caraimatta* are better described as analogous structures, when compared with other tetrablemmid types of conductor (in *Borneomma* and *Choitroblemma*). However, the basally restricted conductor of *Micromatta* is partly embracing the base of complex embolus, while the complex conductor of *Caraimatta* is distinctly separate from the base of the simple embolus.

The vulvae of Mattini belong to two fairly deviating types, while the vulva of *Micromatta* is still unknown. The vulval stem is always thick and strongly sclerotized, and the lateral horns seem to embrace the base of vulval ducts. The lateral horns of at least typical species of Tetrablemini posteriorly support the basal part of vulval ducts. The central process may be present in all Mattini. The inner vulval plate of *Caraimatta* and *Hexablemma* is very large and at least basally wide as in Ablemini. No inner vulval plate has been observed in *Matta*, but its absence can be confirmed only through careful examination of more specimens (only the allotype female of *M. mckenziei* has been available).

Matta Crosby, 1934

Type-species by original designation and monotypy *Matta hambletoni* Crosby, 1934, from Minas Gerais, Brazil.

Medium sized (1.15–1.25 mm) tetrablemid spiders with only two widely spaced eyes that may be practically reduced. Male clypeus long, strongly sloping. Male chelicerae with small boss close to the clypeal margin. Sternal surface throughout reticulate.

Legs relatively long in both sexes. Tarsi long, slightly swollen in basal half, their distal half gradually tapering.

Male palpal tibia strongly swollen. Bulbus short and very wide, rounded triangular. Base of embolus surrounded by complex modifications attached to the bulbus circularly.

Vulval stem thick, lateral horns embracing the base of vulval ducts. Central process membranous. Inner vulval plate not visible in the material examined, but possible present in some form.

Two species known, from southern Brazil and from Mexico.

Matta hambletoni Crosby, 1934 Figs. 297, 300 & 314, Table 3.

Matta hambletoni. Crosby, 1934. Bull. Brooklyn Entomol. Soc. 29: 20, figs. 1–8.

M. hambletoni, Shear, 1978. Amer. Mus. Novit. 2650: 14, figs. 22–23.

Holotype ♂ and allotype ♀ from Brazil, Minas Gerais, Vicosá, 12.V.1930. E. J. Hambleton, in AMNH (New York). Paratypes (2 ♂, 1 ♀ carapace) with same data examined (AMNH).

Male 1.25 mm (not 1.4 mm as indicated in original description), described in detail by Crosby (1934). The cheliceral process is short and conical, situated close

to the base. Clypeus very long and oblique, dorsal part of cephalic area horizontal. Sternum wider than in most species of Tetrablemmidae, except for *Gumasekara ramboda*. Sternal surface distinctly reticulate.

Pulmonary plate finely pitted, postgenital plate long and narrow, with parallel margins. Lateral scutum I anteriorly wide, posteriorly narrower, but reaching lateral to the postgenital plate.

Male palpal tibia strongly swollen and posteriorly with a rounded extension. Bulbus very large, rounded triangular. Embolus originating in the middle of circular complex of ridges. A projecting branch of this continuous ring of modifications has been called a conductor, and thus it is not homologous with the conductor of *Caraimatta* or *Micromatta*. The ejaculatory duct is strongly coiled, and a complex of thin coils is present also in the distal part of the bulbus.

Female (? ca. 1.4 mm), described in detail by Crosby (1934). Clypeus shorter than in male, but the abruptly falling posterior margin of the cephalic area similar to that of male. Legs relatively as long as in male.

Epigynal area not studied by the author, and therefore also the detailed structure of vulva unknown.

Differentiated from all other known tetrablemids by presence of two widely spaced eyes. Differentiated from *M. mckenziei* also by more widely separated cheliceral modifications and details of bulbus.

Matta mckenziei Shear, 1978 Figs. 298, 301, 311–313, Table 3.

Matta mckenziei, Shear, 1978. Amer. Mus. Novit. 2650: 18, figs. 37–39.

Holotype ♂ from Mexico, Campeche, Grutas de San Ignacio, Chencedro, 15 km N of Bolochenticul, 25.VI.1975. D. McKenzie, A. Grubb & R. W. Mitchell Jr., in AMNH (New York), examined; paratype ♀ from Campeche, Actun Halmensura, 5 km E of Cumpich, 31.X.1974. D. McKenzie, J. Reddell, and S. Wiley, in AMNH (New York), examined.

Male 1.15 mm. Described by Shear (1978) and compared then mainly with *M. (=Caraimatta) sbordonii*. He stressed the total absence of traces of eyes, but I could easily see two strongly reduced eyes far from each other, i.e., in a quite similar pattern as in *M. hambletoni*. The legs are long, but not longer than in *M. hambletoni*. The profile of carapace is almost smoothly rounded, and the cheliceral modification consists of two downwards directed central lobes close to the median line. Besides this, there are long basal ridges running parallelly on both chelicerae, and corresponding to the basal knob of various Tetrablemini.

Sternum wide, reticulate, and marginally covered with inwards curved hairs. Dorsal abdominal scutum long oval, hairy. Lateral scutum I anteriorly wide, but posterior part represented by a row of small plates only.

Male palpal tibia slightly swollen, cymbium with very distinct bilobate distal margin. Bulbus basally

very wide as in *M. hambletoni*, but more rounded. Apex of bulbus short, covered by a wide laminar conductor. On the other side of origination of embolus there is a thin membrane with serrate distal edge. Embolus itself is almost straight, distally slightly widened.

Female 1.25 mm. Described by Shear (1978) and stated to be similar to the male in all nonsexual characters. Carapace is slightly lower and the posterior obtuse knob between cephalic and thoracic area is more distinct in female than in male. The anterior part of carapace is distinctly separated from the rest of carapace by a concave depression in female, while the male carapace has smoothly curved, evenly divergent margins. The female chelicerae are short and wide, and the basal ridges are more lateral than in the male. Sternum is relatively narrower in female, and the female postgenital plate is laterally pointed, but parallel-sided in male.

The epigynal area was compared with that of *M. (=Caraimatta) cambridgei* by Shear. The narrow epigynal fold is strongly sclerotized and a wide, distally branching vulval stem is distinctly shining through the integument in the allotype female specimen. In my opinion, it is much different from the epigynal area of all species of *Caraimatta*, but superficially more similar to the vulval type of "*Mono-blemma muchmorei*" from Angelica Rock (fig. 319). However, no central branch of the inner vulval plate can be seen, at least in the single specimen available. This type of vulva without central process and with entirely different type of vulval stem and base of vulval ducts is not easily derived from the vulva of *Caraimatta*, or vice versa. Therefore it may even be possible that *Matta* and *Caraimatta* do not constitute a monophyletic group at all.

M. mckenziei is the nearest known relative of *M. hambletoni* and congeneric with it using all generic standards. These two species are differentiated from each other by shape of carapace and cheliceral modifications as well as by details of genital organs. *M. mckenziei* is differentiated from Mexican species of *Caraimatta* by shape of carapace and relative length of legs, but also by entirely different type of vulva in female and by wide laminar conductor in male.

Micromatta gen. n.

Matta, Shear, 1978. Amer. Mus. Novit. 2650: 18 (in part).

Type-species *Matta atoma* Shear, 1978 from Belize.

Minute (0.95 mm) tetrablemid species with two eyes separated by one diameter from each other. Cephalic area of carapace almost horizontal in both sexes, directly continued by steeply sloping thoracic area. Male chelicerae with no anterior tooth or horn, but with a slightly swollen area anteriorly.

Male palpal femur, patella, tibia, and cymbium unmodified. Palpal bulbus pyriform. Embolus basally wide, distally complex in structure, conductor simple, semicircularly surrounding the base of embolus.

The shape of male bulbus and especially the structure of embolus and conductor are quite different from those of *Matta* and *Caraimatta*. Nongenital characters also much different from the latter two genera. Phylogenetic position in relation to *Matta* and *Caraimatta* unknown, but plesiomorphic structure of male palpal segments proves that it is not paraphyletically arisen from either *Matta* or *Caraimatta*.

Micromatta atoma (Shear, 1978) comb. n.
Matta atoma Shear, 1978. Amer. Mus. Novit. 2650: 18, figs. 40–46.

Holotype ♂ and 6 paratype ♀ from Belize, Belmopan (2.5 miles S), 4.VIII.1972, S. & J. Peck, in CNC (Ottawa), not examined.

Male 0.94 mm, female 0.96 mm. Both sexes described in detail by Shear (1978).

Differentiated from other Mattini by the eye pattern, small size and by details of the genital organs.

Caraimatta gen. n.

Tetrablemma, Bryant, 1940. Bull. Mus. Comp. Zool. 86: 269, not *Tetrablemma* O. Pickard-Cambridge, 1873.

Matta, Gertsch, 1971. Bull. Ass. Mex. Cave Studies 4: 48 & 56.

Tetrablemma, Brignoli, 1972. Proc. Accad. Naz. Lincei, Quad. 171: 130 (in part, *T. cambridgei* and *T. sbordonii* only).

"*Tetrablemma*", Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 86 (probably new genus).

Tetrablemma, Gertsch, 1977. Assoc. Mex. Cave Stud. Bull. 6: 123 (only *T. cambridgei*).

Tetrablemma, Blandin, 1977. Rev. Arachnol. 1: 88 (only *T. cambridgei*).

Matta, Shear, 1978. Amer. Mus. Novit. 2650: 16 (in part).

Type-species *Tetrablemma sbordonii* Brignoli, 1972 from Mexico.

Small (1.0–1.35 mm) tetrablemid spiders with four eyes (sometimes all reduced) in fairly compact group, at least ALE close to each other. Sexual dimorphism in shape of carapace insignificant, male cheliceral tooth small, not pointed.

Male palpal tibia swollen, cymbium distally not bilobate, bulbus elongate pyriform. Ejaculatory duct with a thick coil in the basal part of the bulbus and strongly coiled, thin apical part. Embolus simple, conductor with basal processes and originating separately, but close to the base of embolus.

Vulval stem without lateral horns. Central process present, inner vulval plate with a wide triangular central process, resembling the corresponding structure in Ablemini.

Shear (1978) mentioned several geographically and structurally deviating populations of his two species from Central America and West Indies. There are most probably several species in the material studied in detail by him, but only one new species is described here from material of our museum. All species have been repeatedly confused with each other still within the last ten years.

Caraimatta sbordonii (Brignoli, 1972) comb. n. Figs. 299, 304, 308, 310 & 315, Table 3.

Matta sp., Gertsch, 1971. Bull. Ass. Mex. Cave Stud. 4: 48 (n. sp.) & 56.

Tetrablemma sbordonii, Brignoli, 1972. Proc. Acad. Naz. Lincei, Quad. 171: 10, figs. 1—5 (eyeless ♂ only).

"*T. sbordonii*", Brignoli, 1973. Mem. Soc. Entomol. Ital. 52: 86.

?*T. cambridgei*, Gertsch, 1977. Bull. Assoc. Mex. Cave Stud. 6: 123. The same records from Yucatan (AMNH) were listed under *Matta sbordonii* by Shear (1978), but without reference to Gertsch (1977). Most probably belongs to a related taxon.

Matta sbordonii, Shear, 1978. Amer. Mus. Novit. 2650: 16, figs. 33—36 (♂♀, four-eyed and eyeless populations).

Holotype ♂ from Mexico, Veracruz, Orizaba, Cueva de Ojo de Agua de Tlilapan No 1, 7.XI.1969, V. Sbordonii, in IZR (Roma), examined. Widespread and frequent in Mexico (Shear 1978).

Other material examined: Mexico, Veracruz, Volcan San Martin, 3500 ft, 14.VII.1953. C. Goodnight, in AMNH (New York): 2 ♂ 5 ♀.

Male 1.1—1.15 mm. (Four-eyed population).

Clypeus high, slightly sloping. Four large eyes in strongly recurved row, ALE larger than PLE. The eyeless populations from caves of Veracruz, including the holotype, may belong to same subspecies. Probably some populations with deviating eye-patterns from other parts of Mexico belong to other, undescribed species. The cephalic area is dorsally almost horizontal or slightly concave, ending in a rounded angle.

Chelicerae short and wide, anteriorly with a wide obtuse elevation, but without tooth or horn. Basal ridge obsolete.

Sternum convex, its surface reticulate. Shape of abdominal scutum subcircular to long oval (the same range of variation in both sexes). Lateral scutum I short, posteriorly represented only by a membranous fold or at highest by a few small plates. Remaining lateral scuta wide, especially scutum II. Pulmonary plate without distinct pits. Postgenital plate almost as long as the posterior margin of the pulmonary plate and with parallel margins. Preanal plate with rounded lateral margins.

Male bulbous basally wide, more or less pyriform. Embolus simple, distally slightly modified. Conductor

with a basal notch, a constricted part, and a flat distal lamina that is apically pointed and basally folded. The reservoir is thick and the ejaculatory duct is quickly narrowed to an almost straight distal part. Shear's (1978) figures 34 & 35 depict a bulbous part that has a large distal bulging and the conductor has two basal notches instead of one. The ejaculatory duct in fig. 34 is distally strongly coiled. Unfortunately, Shear did not indicate the locality of the depicted specimen. In my opinion, they seem to represent a different taxon, especially when all the above details of male bulbous seem to agree between the eyeless holotype and four-eyed specimens from Veracruz.

Holotype male 1.35 mm, totally eyeless. Described and depicted in detail by Brignoli (1972), but his measurements are partly erroneous. Carapace $0.60 \times 0.48 \times 0.37$ mm, abdomen 0.80×0.68 mm, leg I $0.52 + 0.16 + 0.42 + 0.29 + 0.32 = 1.61$ mm. It is thus much larger than the practically sympatric four-eyed population studied. The profile of carapace is smoothly rounded, without the rounded angles and intervening horizontal area typical of both sexes of the four-eyed population. Other differences consist of strongly rugose ventral face of femora I in the holotype as compared with the practically smooth surface in other specimens studied.

The male palp of the holotype is both absolutely and relatively much larger than the palp of four-eyed population, but structural differences are quite insignificant. Palpal femur and conductor are both relatively longer in the holotype, but this difference may be due to allometry only.

The differences in shape of carapace, size of all sclerotized parts as well as the relative size of male palpi may be sufficient for establishment of new named taxon for the four-eyed population studied, but the taxonomic status of this population is best settled in connection with a thorough revision of all Central American *Caraimatta*.

Female 1.15—1.2 mm. Profile of carapace more or less similar to that of the male. The sloping angle of clypeus and distinctness of the posterior angle of the cephalic area are slightly altered in well sclerotized specimens when compared with recently moulted specimens, but the differences are parallel in both sexes. The clypeal region of female is separated from the rest of carapace by distinct concave part in dorsal view, while the male carapace has smoothly rounded anterior parts as in most species of Tetrablemmiini and Mattini.

Chelicerae without anterior elevation, but with distinct short basolateral ridge.

Postgenital plate much shorter than in male, anteriorly with a strongly sclerotized fold, reaching around the tapering lateral corners of this plate. Preanal plate with obtusely triangular lateral margins. There are distinct lateral depressions close to the margin, probably fitting to the obtuse elevations of the male chelicerae, but no true pits.

Epigynal area with a small, dark central notch, including the minute epigynal orifice. Vulval ducts relatively much shorter than in *C. blandini*, central branch of inner vulval plate much narrower, almost parallel-sided in its distal part. The vulval structure

of all other populations is unknown, as it was not described or depicted by Shear.

Differentiated from other species of *Caraimatta* by structure of genital organs and from sympatric *C. blandini* also by shape of carapace

Caraimatta blandini sp. n. Figs. 36, 302, 305, Table 3.

Tetrablemma cambridgei, Blandin, 1977. Rev. Arachnol. 1: 86, figs. 1—6.

Holotype ♀ from Mexico, Veracruz, route de Palma Sola à Plan de las Hayas (8 km), Forêt de la Barranca, alt. 170 m, IX.1976, Dans la litière, P. Lavelle, in MZT (Turku); 3 paratype ♀ with same data in coll. P. Blandin.

Female 1.05 mm. Eyes much smaller than in specimens of *C. sbordonii* investigated by me, ALE much larger than PLE. Cephalic region behind the eyes very distinctly raised as far as the obtuse angle separating the cephalic and thoracic areas.

Chelicerae small, besolateral ridge weakly developed. Sternum practically smooth with lower magnifications. Lateral scutum I short, posteriorly continued by a row of small plates. Postgenital plate longer than in *C. sbordonii*, but its anterior margin similarly folded. Preanal plate laterally rounded, without sublateral depressions.

Epigynal area visible as a small dark notch. Vulval ducts very long, vulval stem distinctly surrounding the base of these ducts. Inner vulval plate with a very wide, triangular central branch.

The holotype is characterized by strongly reddish brown colouration, but the taxonomic value of this character is unknown.

Differentiated from the sympatric *C. sbordonii* by smaller size, relatively smaller eyes, and by structure of genital organs.

Caraimatta cambridgei (Bryant, 1940), comb. n.

Tetrablemma cambridgei, Bryant, 1940. Bull. Mus. Comp. Zool. 86: 269, figs. 8—10 & 13.

Matta cambridgei, Shear, 1978. Amer. Mus. Novit. 2650: 16, figs. 24—32.

Holotype ♂ and ♀ paratypes from Cuba, Soledad, 8.VII.1932, Bates & Fairchild, in MCZ (Cambridge), examined.

Male and female described in detail by Bryant (1940), but the size given by her for the male (0.8 mm) is too small. Exact measurements of the type material was not carried out by me or by Shear (1978), but comparison with other species results in size between 0.95—1.05 mm.

C. cambridgei is separated from four-eyed specimens of *C. sbordonii* by longer embolus and details

of conductor in male. The drawing of vulva by Shear (1978) is not complete, but the central branch of the inner vulval plate seems to be quite narrow when compared with *C. sbordonii* and *C. blandini*. The vulval ducts seem to be much shorter than in *C. blandini*.

Shear (1978) listed several records of this species from Jamaica, Costa Rica, and Panama, but suggested also that at least a part of these records may represent new species. Intensive collecting in forest litter of many areas of Haiti in 1978 by the author did not reveal any records of Tetrablemmidae.

Hexablemma Berland, 1920

Hexablemma, Berland, 1920. Voyage de Ch. Alluaud et R. Jeannel en Afrique Orientale: Res. Sci., Arachn. 4: 167, not *Hexablemma*, Simon & Fage, 1922, or Marples, 1955, or Brignoli, 1974 and 1978, or Shimojana, 1977.

Hecablemma, Roewer, 1942. Katalog der Araneae I: 391, error for *Hexablemma* Berland, 1920.

Tetrablemma, Shear, 1978. Amer. Mus. Novit. 2650: 12 (in part).

Type-species by monotypy *H. cataphractum* Berland, 1920 from Kenya.

Small tetrablemmid spiders with a compact eye group of 6 eyes. Surface of carapace and pulmonary plate almost smooth, the latter also pitted. Postgenital plate large, preanal plate of female without modifications.

Epigynal orifice small, on the posterior margin of epigynal fold. Central part of epigynal fold with a distinct, transverse furrow. Vulval stem wide, but without lateral horns. Basal part of thick vulval ducts well sclerotized. Central vulval process sac-like. Inner vulval plate with very long, basally wide central branch.

Male unknown.

In absence of males the phylogenetic position of *Hexablemma* remains uncertain. The vulval structure most resembles that of *Caraimatta*, and as further similarities are present in pattern of ALE & PLE, shape and surface structure of sternum and in the structure of the preanal plate, *Hexablemma* is here listed as a possible African genus of Mattini. The vulval structure definitively excludes a close relationship with *Tetrablemma* suggested by Shear (1978), but a relationship to *Anansia* is not totally out of question.

For suggested male of *Hexablemma*, see p. 74.

Hexablemma cataphractum Berland, 1920
Figs. 295, 303, 306, 307 & 309, Table 3.

Hexablemma cataphractum Berland, 1920. Voyage
... Arachn. 4: 176, figs. 205—210.

Tetramblemma cataphractum, Shear, 1978. Amer.
Mus. Novit. 2506: 12, figs. 18 & 20.

Holotype ♀ from British East Africa (Kenya),
Mt Kenya (1520 m), Blue Post Hotel, 1.1.1912, Ch.
Alluaud & R. Jeannel in MNHN (Paris), examined.

Female 1.25 mm. Four large eyes in strongly
recurved row, ALE bigger than PLE. Two rudi-
mentary eyes behind ALE, resulting in eye pattern
resembling that of many *Ablemma* spp. with rudi-
mentary PME. Carapace and sternum almost smooth
centrally, marginally reticulate. Pulmonary plate
sparsely with small pits, rest of its surface practi-
cally smooth. Postgenital plate laterally tapering,
preanal plate transversely oval.

Female genital pit small, but sparsely sclerotized
circular area at the base of vulval stem may be
confused as representing a large genital pit (cf.
Shear 1978: fig. 18). Vulval structure of the old
holotype strongly bleached, except the strongly
sclerotized distal part of vulval stem. Epigynal
fold with a transverse central groove. Base of
vulval ducts strongly sclerotized along anterior and
posterior margins. Central process long, distally
rounded, but very indistinct in the holotype. Inner
vulval plate obviously completely fixed to the
posterior margin of the pulmonary plate, its central
process very long, gradually tapering.

Tetrambleminae incertae sedis.
Monoblemma Gertsch, 1941

Monoblemma, Gertsch, 1941. Amer. Mus. Novit.
1146, 8.

Monoblemma, Shear, 1978. Amer. Mus. Novit.
2650, 21 (in part).

Type-species by original designation and mono-
typy *M. unica* Gertsch, 1941 from Canal Zone, Pa-
nama.

Minute (0.8) Tetramblemid spiders with only ALE
present (fused to each other in holotype of the
type-species). Carapace low, no sexual dimorphism.
Male chelicerae with a short, but wide anterior
tooth. Male palpus quite simple, bulbus pearshaped,
embolus straight.

Female of type-species unknown, generic affilia-
tion of other possible species doubtful.

The limitation of Shear's (1978) *Monoblem-*
ma is totally changed here. One species is
transferred to the genus *Shearella* (*M. browni*)
and the other one, *M. thorelli*, is
selected as the type-species of a new genus
in the tribe Fallablemini. *M. muchmorei* is

not transferred to any other group, but its
relationship to *M. unica* is only based on
plesiomorphic structure of the male bulbus
and embolus. The same is true for a further
species, *M. becki*, placed into this genus by
Brignoli (1978 b).

Monoblemma unicum Gertsch, 1941
Table 3.

Monoblemma unica Gertsch, 1941. Amer. Mus.
Novit. 1146: 10, figs. 9—12. (♂).

M. unicum, Shear, 1978. Amer. Mus. Novit. 2650:
21, figs 47—50. Emendation of the specific name.

Holotype ♂ from Panama, Canal Zone, Barro
Colorado Island, 9.VII.1938, E. G. Williams, Jr.,
in AMNH (New York), examined.

Male 0.8 mm. Described in detail by Gertsch (1941)
and Shear (1978). Differentiated from all other
species of Tetrambleminae by presence of a single
eye (may be a teratological specimen of two-eyed
species), and also by very small size and smooth
surface.

The low carapace and long oval abdomen combined
with *Shearella*-type of cheliceral horn and quite
plesiomorphic type of bulbus give no useful hints
about final placing of this species.

"Monoblemma" muchmorei Shear, 1978
Figs. 316, 318, Table 3.

Monoblemma muchmorei Shear, 1978. Amer. Mus.
Novit. 2650, 23, figs 51—56.

Holotype ♂ and paratype ♀ from U.S. Virgin
Islands, St. John, 6.VI.1974, W. Muchmore, in
AMNH (New York), not examined. The carapace
of a male paratype from Virgin Islands, Little
Thatch Island, 16.8.1965, Island Project Staff, Uni-
versity of Puerto Rico (AMNH, New York) examined.

Male 0.94 mm, female 1.06 mm. Both sexes
described in detail by Shear (1978).

Differentiated from all other known species of
Tetrambleminae by three pairs of crescent-like
dimples in the thoracic area of carapace of both
sexes.

There are four large eyes, ALE distinctly larger
than PLE, and centrally touching, while the latter
are much further from each other than those of all
Tetramblemma spp. The eye pattern thus resembles
Mariblemma, but also *Caraimatta* in Mattini. The
different number of eyes as such in no argument for
excluding *M. muchmorei* from *Monoblemma*, but the
high carapace, short and robust legs, very wide
sternum, and different type of cheliceral modification
of male all support the absence of close relationship
between *M. unicum* and *M. muchmorei*. The cheli-
ceral horn was depicted by Shear as an almost

straight, conical process, but it seems to a down-
wards curved hook in profile. The horns of both
chelicerae are distally close to each other in *M.*
muchmorei, but more divergent in all other Tetra-
blemini, except probably *Rhinoblemma unicornis*.

The palpus is relatively large, rounded triangular
or almost pyriform. Embolus is long and almost
straight, unmodified. The whole palpus consists only
of extremely plesiomorphic details as does that of
M. unicum. Thus phylogenetic relationships cannot
be discussed at all for similarities of male palpi. In
spite of being quite simple, the palpi do not look
similar — the palpus of *M. unicum* is also much
smaller.

"Monoblemma" sp.
Figs. 317, 319, Table 3.

Monoblemma muchmorei Shear, 1978. Amer. Mus.
Novit. 2650, 23 (in part).

A female specimen from Virgin Islands, Angelica
Rock off Cooper Island, 26.V.1966, IPS/UPR
(AMNH, New York) has been examined, but it
could not be directly compared with the female
paratype from the type locality of *M. muchmorei*.
Thus it has not been named here, although it seems
not belong to *M. muchmorei*.

The eyes of this specimen are much smaller than
those of the male paratype of *M. muchmorei* and the
characteristic crescent-shaped dimples on the cara-
pace are absent. The carapace is also relatively much
longer in this female specimen, but this difference
could be explained by sexual dimorphism. In
contrast, the longer and more slender legs of the
female support my hypothesis that these two speci-
mens examined are not conspecific.

Similar profile of carapace and the same type
of sternal surface and sternal shape seem to show
that these specimens most probably belong to the
same genus or at least are distinctly related.

The vulva of this *"Monoblemma" sp.* has no well-
defined lateral horns of the vulval stem, and the
whole structure of ducts is reminiscent of corres-
ponding parts of the vulva of *Caraimatta* spp., but
the central branch of the inner vulval plate is
narrow as in all typical species of Tetramblemini.

"Monoblemma" becki Brignoli, 1978

Monoblemma becki Brignoli, 1978. Beitr. Naturk.
Forsch. Südw. Deutschl. 37: 143, figs. 2—5.

Holotype ♂ from Brazil, Amazon region, sur-
roundings of Manaus, Reserva Ducke, 21.XII.1965.
L. Beck, in LNK (Karlsruhe), not examined.

Male 0.86 mm, described in detail by Brignoli
(1978 b). This species was included in *Monoblemma*
mainly because of simple bulbus of the palp. How-
ever, this character is plesiomorphic in Tetramble-
minae and cannot prove any phylogenetic re-

lationship. On the other hand, a comparison of all
the details of male palpi, including shape and relative
length of palpal femur and tibia, shape of basal
part of the bulbus, course of ejaculatory duct and
reservoir, apex of embolus, and relative length of
the rounded triangular bulbus, seem to prove that
the differences, although never striking, are not at
all typical of closely related congeners of Tetra-
blemmidae.

The lack of male cheliceral horn and different
profile of the eyeless carapace further prove that
this species most probably is neither congeneric with
Monoblemma unicum nor with *"Monoblemma"*
muchmorei. A new genus is the most probable placing
for *"Monoblemma" becki*, but the defective infor-
mation of all *Monoblemma* and *"Monoblemma"* spp.
must be essentially completed, before a more final
revision of these species is possible. They are cer-
tainly not related to any genus occurring in the
Oriental-Australian region.

Maijana gen. n.

Tetramblemma, Simon, 1905. Mitt. Naturh. Mus.
Hamburg 22: 56, not O. Pickard-Cambridge, 1873.

Type-species *M. racki* n. sp. from Java.

Minute (0.9 mm) pale tetramblemid spiders with
four eyes in compact group and cephalic area ending
in sharp angle in female. Sternum wide, reticulate.
Pulmonary plate finely reticulate, no transverse
furrows or widened hair pits present. Preanal plate
without pits.

Epigynal fold thick, vulval stem without lateral
horns and central process. Inner vulval plate not
trifurcate, but its anterior margin with a short and
wide, convex extension.

Males unknown.

The vulval structure of the single known
species of this genus is quite different from
all other known Tetramblemmidae. The com-
pact eye pattern seems to exclude a phylo-
genetic relationship to Fallablemini or
Brignoliellini. The tribe Mattini is excluded
from discussion on zoogeographical grounds,
but there are neither any similarities in the
structure.

The vulva of *Ablemma* has no single detail
that could be compared with that of *Maijana*,
except the absence of central process. The
females of the other known genus, *Sulaimania*,
are not known, but smooth surface and enti-
rely different patterns of eyes and abdominal
scuta definitively exclude relationship of
Sulaimania and *Maijana*.

The structural variation within Oriental-
Australian Tetramblemini is wider than in

other tribes, but the vulva of *Maijana* cannot be derived from structural types of known genera. The vulva of *Shearella* and related genera shares the tendency of reduction of central process and central branch of the inner vulval plate with *Maijana*, but the resulting vulva is not at all similar, and the general appearance as well as the eye pattern of *Maijana* are not at all similar to *Shearella*.

The presence of an unknown evolutionary line within Oriental-Australian Tetrablemmidae is possible, but not the most probable alternative for placing of *Maijana*. It may be a strongly apomorphic relative of Tetrablemini or even Ablemini.

Maijana racki sp. n.
Figs. 320–324, Table 3.

Tetrablemma medioculatum, Simon, 1905. Mitt. Naturh. Mus. Hamburg 22: 56, not *T. medioculatum* O. Pickard-Cambridge, 1873 (♂).

Holotype ♀ from Java, Buitenzorg, Tjompoe (= Indonesia, Jawa Barat, Ciampea), by sieving bat guano in cave, 11.III.1904, K. Kraepelin, in ZMH (Hamburg), examined.

The two known caves in Ciampea (Gua Silenggang & Gua Sibiuk) were thoroughly investigated by the author in October 1979, and among various other microhabitats large amounts of bat guano were investigated without any specimens of Tetrablemmidae. It is possible that the holotype of *M. racki* was quite coincidentally collected in the cave.

Female 0.9 mm. Carapace with almost horizontal cephalic area, ending in a sharp, short tooth. Eyes small, subequal, PLE separated by less than one diameter. Chelicerae short, basolateral ridge very small and insignificant. Sternum wide, posteriorly widely obtuse, all over strongly reticulate. Dorsal abdominal scutum oval, but its anterior margin straight. Lateral scutum I very short. Postgenital plate wide, with parallel margins, perigenital plates minute. Preanal plate trapezoidal, posteriorly narrowed.

Epigynal fold wide, its margins parallel almost the whole length of the posterior margin of the pulmonary plate. The whole fold looks darker than surrounding plates because of wide sclerotized vulva. Epigynal orifice not externally visible. Vulval stem without lateral horns and central process, but central part of very wide sclerotization with three widely rounded anterior extensions. The middle extension is wide and slightly convex, and it may be regarded as homologous with the central part of the inner vulval plate of other Tetrablemmidae.

Externally not radically different from small *Tetrablemma* spp., but vulva quite unique, and a

more detailed comparison of all structural parts easily differentiates this species from all other known minute Tetrablemmidae. The confusion by Simon (1905) is easily understood, as he did not compare his female specimen with the male of the only known minute species of Tetrablemmidae.

Tetrablemmine sp.

Hexablemma cataphractum, Simon ? Fage, 1922. Arch. Zool. Expér. Gen. 60: 542, fig. VII: 1–3, not *H. cataphractum* Berland, 1920.

A male tetrablemmid specimen from British East Africa (=Kenya), Province of Seyidié, Shimoni Cave, leg. Ch. Alluaud & R. Jeannel, was supposed to be the unknown male of *H. cataphractum* by Simon & Fage (1922). The specimen may be lost now, or at least it has not been found in MNHN (Paris). Shear (1978) doubted the conspecificity of this male specimen with the female of *H. cataphractum*, but the latter was simultaneously included in *Tetrablemma*.

As long as the males of the genus *Hexablemma* are not known, there is a possibility that this cave species from coastal Kenya is somewhat related with *Hexablemma*, although hardly conspecific. *Hexablemma* is included in Mattini and a short cheliceral horn and basally modified embolus is characteristic of males of this tribe.

On the other hand, the modification of male palpal tibia and femur suggest relationship with the genus *Gunasekara*, a geographically close six-eyed genus of Tetrablemini. *Mariblemma* and *Shearella*, both certainly close relatives of *Gunasekara* share a short and thick cheliceral horn with this Kenyan specimen, and basal modification of embolus is also present in *Gunasekara*. A short male palpal femur is further characteristic of two other African genera. *Cuango-blemma* and *Anansia*. In strict contrast to the case of *Maijana racki*, many geographically near genera of African tetrablemmids probably are not yet described, and thus this Kenyan male specimen may even belong to some other group.

Most probably this specimen belongs to an undescribed species, but I leave it unnamed until the male of *H. cataphractum* will be known.

4. Taxonomic value and evolution of morphological characters

4.1. Tetrablemmidae

Tetrablemmidae belongs to a line of spider evolution in which the practical diagnostic characters as well as many significant characters used in phylogenetic classification are different from those used in the taxonomy of most spider families within Araneomorpha and Amaurobiomorpha (both sensu Lehtinen 1978).

The male palpus of Tetrablemmidae is simple, but there are many minor modifications to the basal segments. Most of them may have developed as the result of parallel evolution within Tetrablemmidae, as similar minor modifications have certainly evolved independently in other families of Sicarioidea and even in Ctenizoidea and Theraphosoidea. Apomorphic types of the tetrablemmid bulbus afford many useful characters, but on the whole the male palpus alone cannot be used in definition and delimitation of most supra-specific taxa in Tetrablemmidae.

The external genital characters of the female are more complex in Tetrablemmidae than in most Sicarioidea, Ctenizoidea, and Theraphosoidea. However, the interpretation of parallel evolution of some striking characters in this area is difficult, and has resulted in unjustified limitation of Tetrablemmid subfamilies by Shear (1978). The distal parts of the seminal receptacula are soft in Tetrablemmidae, and they can hardly have any practical value in the taxonomy of this group.

In contrast to most spider groups, including other groups of Theraphosomorpha, Tetrablemmidae has several groups of structural, non-genital characters that seem to have much practical value in both routine identification of species and in delimitation of supraspecific taxa. These characters include complex patterns of abdominal scuta, sexual dimorphism of carapace, chelicerae, and legs. The eye patterns and surface structure of all sclerotized parts are, as in any group of spiders, additional, useful non-genital characters.

During the first hundred years of Tetrablemmid taxonomy taxa of various levels were created and described with practically no

comments on the value of the characters used. This led to curious delimitations of some genera, and especially *Paculla*, *Hexablemma*, and *Tetrablemma*.

Shear (1978) presented a cladogram of Tetrablemmid genera known to him. This was argued by suggested evolution of 22 different characters. I am in total agreement with him with regard to evolution of his characters 1–7 dealing with separation of the whole group (Tetrablemmidae and Pacullidae sensu Shear) from other spider families, as well as with separation of Pacullinae and Tetrablemmidae, although Shear treated these groups as families.

Shear (1978) personally studied only three related species of Pacullini, and thus had no opportunity for detailed discussion of the taxonomic value and evolution of characters within Pacullinae. In my opinion, the evolution of many characters in Pacullinae is largely different from the evolution of the same characters in Tetrablemmidae. Therefore the discussion of taxonomic value and evolution of morphological characters is presented separately for both subfamilies. It is obvious that Pacullinae and Tetrablemmidae are true sister groups, and thus none of them can be regarded as a more apomorphic branch of a paraphyletic, plesiomorphic group. In fact, the plesiomorphic state of some characters in Pacullinae may simultaneously be the apomorphic state in Tetrablemmidae (type of surface structure), and vice versa (possibly the position of metatarsal trichobothrium). Both subfamilies are characterized by strange modifications of the carapace. They are, however, not sex-linked in Pacullinae, but are strictly so in Tetrablemmidae.

I have tried to follow the evolution of the combined characters 8–22 from Shear's cladogram throughout the whole group discussed, whereas Shear has used many characters at a single point of divergence. In my opinion, an oscillating type of structural change in complex structures is very unlikely, especially within Tetrablemmidae, while minor adaptive changes (thickening of palpal

tibia, tapering apex of bulbus, widening of the posterior fold of the pulmonary plate, etc.) have most probably occurred and disappeared repeatedly during the evolution of any large family, including Tetrablemmidae.

4.2. Pacullinae

Despite the scarcity of known species in Pacullinae, the creation of an indisputable cladogram is not yet possible. Some of the most distinct morphological characters of Pacullinae are discontinuously apomorphic, while the polarity of evolution is not known for some other characters.

Modifications of carapace

The shape of carapace, pattern of eyes, and surface structure of carapace and other sclerotized parts are much less variable within all taxa of Pacullinae in comparison with the wide variation between different genera of Tetrablemmidae.

Sexual dimorphism in the carapace of Pacullinae is restricted to the presence of a conical tooth at the clypeal margin of male *Perania* spp.

A very rugose type of chitinous surface is present in all known species of Pacullinae, and this pattern may be the plesiomorphic state in recent Pacullinae, although the rugose type is certainly apomorphic in recent Tetrablemmidae. The evolution of these two subfamilies may have followed different trends for long periods. The presence of a posterior sternal process in practically all Pacullinae is an additional result of this tendency to rugosity, and its exceptionally weak development in *Mirania* may be an apomorphic reduction.

The shape of modified hair pits in Pacullinae seems to be a phylogenetically significant character, and it is also detectable in quite juvenile specimens. The simple or triangular, swollen outer margin of pits most probably represents a plesiomorphic state (*Perania* and *Mirania*), and the starlike modifications may be synapomorphic for *Sabahya*, *Lamania*, and "some" *Paculla*. The monophyly of the latter

genus is not confirmed, and additional contradictions are afforded by the different modifications of the legs in males.

The most problematic character of the paculline carapace consists of the presence of the paired, strong teeth in the thoracic area of many species that are certainly more related to toothless species than to each other. Such rigid teeth of the thoracic area are rare, but not unknown, in other groups of spiders. The paired teeth in the Oonopid genus *Xyphinus* may be partly homologous (controlled by genes at the same loci), while the paired spines of *Eleleis* (Amaurobiomorpha: Prodidomidae) and various unpaired or partly paired spine patterns of Araneidae (Araneomorpha) cannot be discussed seriously in this respect.

The paired thoracic teeth occur in four different genera of Pacullinae (*Mirania*, *Paculla*, *Lamania*, and *Sabahya*), and the four known species (type-species of these genera) do not share any phylogenetically significant additional characters as is easily understood by the generic limitation chosen here. This character cannot be regarded as synapomorphic but, however, it is certainly homologous in all these four species. Neither can it be regarded as plesiomorphic for Pacullinae as it is absent in *Perania* with its quite plesiomorphic type of male genital organs, and probably in generally more plesiomorphic representatives of *Paculla* and *Lamania*. These paired teeth are similar in both sexes of *Lamania nirmala* and probably similar in *Mirania armata* (female holotype lost), but slightly stronger in males of *Sabahya kinabaluana*. The female of *Paculla granulosa* is not known.

The above-described discontinuous pattern of a synapomorphic character can perhaps be compared to the parallel structural patterns in the genital organs of the genus *Drosophila* (Throckmorton 1962). They are probably controlled by a group of genes, and more than one gene is needed to realize the pattern, for which a basic gene pool is present in a large group of Pacullinae. This kind of discontinuous variation has been regarded as some kind of evolutionary trend on a small scale, previously known in spiders in the Erigonid tribe Diplocephalini, but combined there with polymorphism. (Lehtinen 1979).

Abdominal and leg characters

The evolution of the pattern of abdominal scuta in Pacullinae is entirely different from that in Tetrablemmidae, but still imperfectly known.

The dorsal abdominal scutum is convex, thin, and completely hairy only in *Paculla sulaimani*, a species with male genital organs similar to those of *P. granulosa*. The latter species, as well as all remaining Pacullinae, have a thick abdominal scutum with large hairless, variably sculptured margin, and the central part sparsely covered with very thin hairs without distinct pits and variably modified unevenness of the surface. This pattern is easily classified as synapomorphic, and this opinion is strengthened by the further apomorphy of the reduced scutum in *Perania*. However, the plesiomorphic state in *P. sulaimani*, similar to the common type in Tetrablemmidae, does not fit as such into normal Hennigian cladistics. The only explanation seems to me to be that the plesiomorphic pattern is atavistic. There may then be a genetic basis for an apomorphic type of scutum, but its development is prevented by an inhibitory gene or by a lack of one of the necessary genes in a system of multiple genes.

The evolution of ventral and lateral scuta in Pacullinae is surprising. There is a distinct sexual dimorphism pertaining to number, size, and structure of these scuta. The reduction of both ventral and lateral scuta is certainly a synapomorphy in *Perania*, and is also correlated to the reduction of the dorsal scutum. The ontogeny of the abdominal scuta (cf. p. 23) shows that this reduction can also be classified as neoteny.

The posterior branching of lateral scuta seems to be a trend within Pacullinae, and the exact pattern of branching can only possibly be directly used as a measure of phylogenetic relationship. This branching reaches its known maximum in the male of *Mirania armata*, but too few specimens of Pacullinae are known to be able to describe the infraspecific variation and detailed phylogenetic value of this character.

The modification of the first leg of the male is a very common type of sexual dimorphism in all main lines of spider evolu-

tion. Various minor modifications occur sporadically in both Tetrablemmidae and Pacullinae, and it is impossible to construct any cladograms based only on such characters. The metatarsal spicules of *Perania* and *Mirania* are synapomorphic, and not strictly homologous to the short spines in the first legs of males in *Sabahya kinabaluana* and *Paculla cameronensis*.

The trichobothrial pattern within Pacullinae is much more variable than in Tetrablemmidae, but only concerns the position of the metatarsal trichobothrium and the reciprocal position of the prolateral and retrolateral rows of tibial trichobothria. The position of trichobothria is generally a distinctly allometric character in spiders (Lehtinen, 1980a), and thus this character is strongly correlated with variable relative length of legs in Pacullinae. The latter character is again mainly adaptive throughout, not only for spiders, but also Arthropoda in general.

Chelicerel characters

The anterior face of the chelicerae is unmodified in both sexes of all species of known Pacullinae, in strict contrast to the strong sexual dimorphism in Tetrablemmidae.

The base of the fang is unique in Pacullinae, when compared with all other families with the triangular chelicerel lamina (Sicarioidea, Filistatidae, Pholcidae, etc.). The presence of teeth between the fang and the lamina is synapomorphic for all Pacullinae, if the uneven keel of *Perania* and irregular rugosity of this area in *Mirania* are regarded as structures homologous with the distinct teeth in *Paculla*, *Lamania*, and *Sabahya*. There are no well-defined teeth in the tetrablemmine chelicerae, but the area between the base of the fang and the chelicerel lamina is notched or otherwise slightly modified in males of various Tetrablemmidae spp., and most strongly in Brignoliellini (cf. Figs. 74, 102, etc.).

Genital organs

The polarity of evolution in the male genital organs of Pacullinae is easily confirmed. The

cymbium of *Perania* and *Mirania* is of the same plesiomorphic type that is common in most spider families of most main lineages. Thus it is impossible to derive Peraniini from Pacullini, although a large number of other characters in Peraniini are apomorphic when compared with the same characters in Pacullini. The most apomorphic type of cymbium and palpal tibia is found in *Sabahya*.

The type of bulbus and the general design of the embolus is a good diagnostic synapomorphy for Peraniini and for the genus *Lamania* separately, while the genus *Sabahya* represents a third, very apomorphic type.

The structure of the embolus in *Paculla*, as this genus is provisionally delimited here, is difficult to assess for the purposes of phylogenetic relationship. As stressed before, the emboli of *P. granulosa* and *P. sulaimani* are similar, while the emboli of the remaining species of *Paculla* are simple enough to be classified together with the two firstnamed species. However, their simplicity is rather a proof of their plesiomorphy within Pacullini than a proof of their congenerity with the type-species. Additional *Paculla* material is necessary for more detailed discussion of its final monophyly.

The evolution of the female genital organs remains even more obscure than that of the male. This is mainly due to lack of sufficient information and material. The female genitalia of *Perania* spp. could be studied only superficially, the female holotype of *Mirania armata* has been destroyed, and no females are known for three of the four species of *Paculla*, including the type-species. The structural variation within the female genital organs of the small subfamily Pacullinae is most probably exceptionally great, as preliminarily concluded from the three fundamentally different types of vulval plate within the single tribe Pacullini.

There is an external "epigynal area" in both species of *Perania* and their shapes seem to be significantly distinct. Actually this epigynal area consists of a depression of the surface of the pulmonary plate close to the main course of the internal vulval structures, which seem to be large and consisting of a distinctly modified inner vulval plate. These large modifications shine through the integument as

dark, continuous, paired structures, corresponding to similarly large paired structures in *Sabahya*. The above-mentioned "epigynal area" of *Perania* is not connected with the internal structures by any orifice, but is situated far from the margin of the pulmonary plate. In fact, the structure of female genital orifices is totally unknown in Peraniini; they may be unpaired or paired.

The epigynal orifice of *Paculla negara* (the only known female *Paculla* and possibly not close to the type-species) is paired, but the large orifices are separated only by a thin, sclerotized septum. As other characters support the relative plesiomorphy of *Paculla* within Pacullini, this paired type is tentatively regarded here as the plesiomorphic state within Pacullini. *Sabahya* with small, paired, but widely separated genital orifices and *Lamania* with a large, central, unpaired orifice would then represent two different apomorphic types. This is further supported by the fact that the female genital orifices are usually paired in most main groups of spiders and also in other groups of Sicarioidea, including Diguettidae. The small, unpaired female genital orifice in Tetrablemmiinae is situated within the pulmonary plate and not behind it as in Pacullinae. Thus the unpaired orifices in Tetrablemmiinae and Pacullinae are not homologous, and they represent two independent, different apomorphic states of this character.

The inner vulval plate of Pacullinae together with the more or less membranous part along the inner surface of the pulmonary plate constitutes a sclerotized, tubular structure. In this paper the sclerotized dorsal parts of this tube are simply named the inner vulval plate, without positive or negative hypotheses concerning its homology with the inner vulval plate of Tetrablemmiinae. Both are inner, sclerotized structures, at least partly attached to the inner face of the posterior margin of the pulmonary plate.

The vulval plates of all known species of *Lamania* are surprisingly similar, while the vulval plates of both *Paculla negara* and *Sabahya kinabaluana* include specialized structures, obviously as adaptations to copulatory functions with two types of entirely different embolic division.

The construction of a cladogram of the

type-species of all paculline genera is easy, but the placement of other species of *Paculla* into that scheme of cladistic classification poses problems. The genus *Paculla* is probably polyphyletic but no unequivocal cladistic division is possible with the scanty material available.

Ultrastructure

The ultrastructure of most important chitinous parts of Tetrablemmidae has only been described for one species of Pacullinae and a few species of Tetrablemmiinae. It has been used to test the position of the whole family in the system of haplogyne spiders, but until now no attempt has been made to use ultrastructural characters of all genera for cladistics within the family. Cf. notes on p. 9.

4.3. Tetrablemmiinae

Eye patterns

The eye pattern of Pacullinae and two tribes of Tetrablemmiinae (Brignoliellini & Fallablemmiini) is identical to that of Diguettidae, Segestriidae and many other groups of Sicarioidea and other haplogyne groups of Theraphosomorpha. It is therefore certain that all other eye patterns within Tetrablemmiinae are apomorphic. With reference to Oriental-Australian groups only, the suggestion that all these apomorphic patterns are evolved from a single, compact type of eye pattern that is shared by most Ablemmiini and Tetrablemmiini can be well argued. All Oriental-Australian tetrablemmine species with reduced number of eyes have ALE close to each other, while the reduction of PME always precedes that of PLE. The relative position and size of PLE has changed according to slightly different trends in Ablemmiini and three groups of Tetrablemmiini. The poorly known Neotropical fauna makes this possible synapomorphy of all derived eye patterns uncertain. The ALE of *Matta* are well separated from each other, and also, but less distinctly, in *Micromatta*, while the third known genus of

Mattini, *Caraimatta* and "*Monoblemma*" *muchmorei* have ALE close together, and their entire eye pattern strongly resembles that of four-eyed *Shearella*, *Mariblemma*, and Ablemmiini (some *Bannia* spp.) It is possible that the ALE of *Micromatta* and *Matta* have been secondarily separated. If so, the hypothesis of synapomorphy of all derived eye patterns in Tetrablemmiinae is correct, but an alternative explanation of parallel evolution towards closely spaced ALE, at least in one line of evolution within the Neotropical region must be borne in mind.

The single eye in *Monoblemma unicum* is simply the result of fusion of a pair of ALE.

Sexual dimorphism

The sexual dimorphism is quite insignificant in Pacullinae, and the evolution of these patterns in the two subfamilies of Tetrablemmidae has nothing in common.

The sexual dimorphism in Tetrablemmiinae is quite striking and usually affects the general shape of carapace and chelicerae, size and shape of dorsal abdominal scutum, pattern of ventral and sometimes even lateral abdominal scuta, and length of legs. Projecting horns or teeth occur on the carapace and chelicerae of many groups of tetrablemmine males. Modifications of the tibiae, metatarsi, or tarsi in leg I of the male has evolved in parallel in a few groups, while modification of the male gnathocoxae is significant only in the genus *Gunasekara* (Tetrablemmiini).

Interpretation of synapomorphic patterns in modifications of the male carapace and chelicerae is sometimes difficult, in spite of the fact that these modifications are the best diagnostic characters for many genera.

A low carapace in both sexes is certainly a plesiomorphic pattern in both Tetrablemmiinae and Pacullinae, but a modification typical of some group may be inhibited by mutation of a single gene, and thus a phenotypically primitive type is not always necessarily a proof of plesiomorphy. Unmodified or slightly modified (without projections) male carapaces are found in practically all tribes and groups (*Fallablemma*, *Indicoblemma*, *Pahanga*, *Mariblemma*, *Tetrablemma* (*Kuma-*

onia), *Micromatta*, *Monoblemma*). The most totally apomorphic tribe is Ablemini, but even here the modifications of *Sulaimania* are not striking. If we suppose that each unmodified genus of the above list is really plesiomorphic, the modification patterns of each of the tetrablemmine tribes have evolved independently, although following some common trends, for which a genetic basis must have been present as long as sexual dimorphism of the male carapace has been characteristic of Tetrablemmineae.

The exact homology of clypeal horns or protuberances in *Choirolemma*, *Brignoliella*, *Rhinoblemma*, and *Cuangoblemma* can neither be proved nor rejected, but this problem is not significant in practical taxonomy of Tetrablemmineae. Each of these genera certainly has close relatives without clypeal horns. The swellings immediately below the ocular area in *Borneomma* and the small protuberances of the hump of the cephalic area in *Tetrablemma medioculatum* are different manifestations of the same trend, although probably not strictly homologous with the clypeal modifications of *Brignoliella* and *Rhinoblemma*, respectively.

The exact homology of different modifications of the male chelicerae is difficult to interpret, and similar types of modifications have probably been produced through parallel evolution in several tribes. The presence of an anterior cheliceral horn or tooth in the male is a general trend in Tetrablemmineae, although such modifications are unknown in Pacullinae. It is impossible to decide whether the few groups with unmodified male chelicerae (*Singaporemma*, "*Monoblemma*" *becki*, and *Micromatta*) all represent a plesiomorphic state or whether some of them represent only a suppressed phenotype of an otherwise modified group. The shape of this horn or tooth is often quite simple and e.g. the basally thick, short horns of *Shearella*, *Monoblemma*, and *Pahanga dura* could be interpreted as proof of a close relationship, if the evolution of all other characters is excluded. However, the wide range of types of male cheliceral teeth in the otherwise fairly uniform, large genus *Brignoliella* proves that the shape and exact position of this modification can easily be different even in closely related species.

The long, curved cheliceral horn of *Tetrablemma* has been generally regarded as a good synapomorphy for this genus. However, the long cheliceral horns in other genera (*Gunasekara*, *Cuangoblemma*, and *Anansia*) are not fundamentally dissimilar, although they differ in the structure (*Gunasekara*) or direction of the apex. The small cheliceral horn of many Brignoliellini, both primitive and advanced, is evidently a homologous structure in this tribe and possibly also a useful synapomorphy for the whole tribe. However, the insignificant anterior cheliceral modifications in Fallablemini may also be homologous with them. The distal tooth in the male chelicerae of *Ablemma* (*Bannia*) is certainly homologous with the subdistal — subcentral tooth of other Ablemini, and may therefore be homologous with the anterior cheliceral modifications of some other tribe, too.

The cheliceral modifications of the male are correlated with modifications of the female preanal plate in at least Brignoliellini and Ablemini. In all genera of these tribes with these modifications, the function of these correlated structures is the same: the male cheliceral teeth fit into pits or grooves in the female preanal plate. The long cheliceral horns of Tetrablemini must function differently because no pits are present in female preanal plates of this tribe, except for the anterior grooves in *Singalangia sternalis*. The male of this species, which seems to be related to *Tetrablemma*, is unknown.

Summarizing the above facts, it is evident that the male cheliceral modifications and correlated modifications of the female preanal plate constitute a group of characters that is mostly useful in the separation of closely related species, and is often, but not always, important in the study of phylogenetic relationships within Tetrablemmineae.

Another group of sexually dimorphic characters with corresponding structures in the female consists of modifications of the carapace of the male fitting into a pit or concavity in the female sternum during copulation. It is diagnostic for the whole tribe Ablemini, but a parallel case is found separately in

Anansia astaroth, a member of Tetrablemini.

The pattern and shape of the abdominal plates includes several, more or less sexually dimorphic characters. The dorsal abdominal plate is often relatively longer in the male or at least the variation in shape is much greater in the female.

The female pulmonary plate always has a fold along the posterior margin, while there is usually no fold in the male. The shape and especially the width of the central part of this epigynal fold is quite variable, but fairly similar in groups of related species. Thus it has been centrally widened and/or thickened several times during the course of tetrablemmine evolution.

The postgenital plate is always longer and often wider in males, but its margins may be thickened or otherwise slightly modified in many females. This pattern of sexual dimorphism is the opposite of that found in the Pacullinae.

The modification of the preanal plate of females was mentioned above with regard to the locking pits. However, the shape of this plate may also differ slightly between males and females, but the differences are apparently correlated with the presence of pits.

The pattern of reduction of the lateral scutum I sometimes differs between males and females, but there is no general rule for these differences. On the other hand, the number of perigenital plates is often larger in females, corresponding to the shorter postgenital plates.

The patterns of modification in the first pair of male legs are not phylogenetically important in Tetrablemmidae, and such modifications are known in a large number of spider families representing all main groups of spiders.

The first tarsi are slightly swollen or distally tapering in *Borneomma*, *Matta*, and some species of *Ablemma* (*Bannia*). The metatarsal modifications of two species of *Tetrablemma* s. str. are certainly synapomorphic, while metatarsal modifications of two other species of Tetrablemini, *Gunasekara ramboda* and *Tetrablemma* (*Kumaonia*) *loebli*, must be classified as parallel autopomorphies. In the third subgenus of *Tetrablemma*, *Indonops*, the mo-

dification concerns the male tibia I. The modifications of the first leg in the male are entirely different in Pacullinae, but their distribution is also scattered.

The relative length of legs in males is usually greater than in females both in Pacullinae and Tetrablemmineae, but the same is true for almost every family of spiders.

Patterns of abdominal scuta

The presence of four ventral, four pairs of lateral, and four posterior scuta has long been used as a diagnostic character for the whole family and Shear (1978) described the exact relative size and shape of some of the plates as specific characters. However, the phylogenetic relationships between supra-specific taxa of Tetrablemmineae and Pacullinae has not been discussed on the basis of patterns of the abdominal scuta.

The relative size and shape of the pulmonary plate is naturally correlated with the shape of the whole abdomen. Large variations occur within single, well-defined genera such as *Tetrablemma* and *Ablemma*. The anal plate is less variable than the other ventral plates, and until now its shape and relative size has never been used as a diagnostic character.

The relative sizes and shapes of the postgenital and preanal plates are the most practical taxonomic characters in this group of characters. The most deviant patterns are found in *Sulaimania* (both subequal in width) and *Singalangia* (postgenital plate reduced in females, preanal plate very wide). The large postgenital plate of *Singaporemma* as well as the long, wide postgenital plate of *Anansia* are practical generic characters.

The width of all lateral scuta is typical of *Anansia*, *Caratmatta* and *Shearella* but most of the significant variations in the lateral scuta are concentrated on the extremely variable lateral scutum I (the most ventral).

A long, but narrow, completely sclerotized lateral scutum I is typical of all pitted genera of Brignoliellini, while the otherwise more plesiomorphic *Indicoblemma* and *Chavia* have a short anterior plate, followed by a very distinct, posterior row of small plates, and the lateral scutum I is totally reduced in

Singaporemma. A parallel pattern of reduction is found in Tetrablemmmini, where a total reduction has taken place independently in *Singalangia*. However, the distinctness of the small posterior plates is quite variable within *Tetrablemma* (no small plates in *T. samoensis*, anterior and posterior continuous plates in *T. deccanensis*, and short anterior plate followed by a row of small posterior plates in most other species). The posterior part is represented by only a membranous fold in many, not closely related species or groups of species.

The anterior end of the lateral plates has usually retained the plesiomorphic pattern: IV longest, III shorter, II shortest, I as long as IV or slightly shorter. However, this pattern is sometimes altered (probably due to adaptation to short and wide abdomen), and the anterior ends of all plates may constitute a more compact group, but even then IV and I are slightly longer than II and III (*Borneomma*).

The anterior of the abdomen normally has no plates between the dorsal and pulmonary plates, but the hairy margin of the pulmonary plate is often separated into a row of a few minute plates, each with a hair, especially in Brignoliellini.

A detailed statistical analysis and a large amount of exact measurements are still necessary to finally clarify the phylogenetic value of various characters in this character group. Most drawings of abdominal plates of Tetrablemmnae by previous authors are quite inaccurate with regard to relative size and shape of the single plates. They have most probably been drawn only to show the number of main plates.

Surface structure of sclerotized parts

This group of characters was represented in Shear's cladogram by "cuticle of carapace" — 8 and "cuticle of ventral plates" — 11. This is perhaps the most misleading part of his analysis of the taxonomic value of characters. Detailed analysis of all tetrablemmid material available to me has led to the following conclusions about these kinds of character.

The surface structures of carapace, sternum,

and pulmonary plate are modified independently of each other. The surface structure of the dorsal abdominal scutum is only slightly different in different groups of Tetrablemmnae, and in most cases its phylogenetic value is quite insignificant, because no clear-cut types are present. There is only continuous variation of the distinctness of the hair pits and continuous variation of the intervening surface from extremely finely reticulate to very distinctly reticulate.

The surface of juvenile and subadult specimens is reticulate on the sternum of all groups and smooth or very finely reticulate in the carapace and abdominal plates. Unfortunately, no juveniles of *Monoblemma*, *Sulaimania*, or *Cuangoblemma* were available for study; adults of these genera have the smoothest surface on all parts. In my opinion, a reticulate surface pattern on all parts is plesiomorphic for Tetrablemmnae. All pitted and also smooth patterns represent apomorphic patterns evolved in different directions. Even the exceptionally strong reticulate pattern of all sclerotized parts in *Singaporemma* is a third type of apomorphy.

The strongly pitted sternum (and sometimes partly pitted carapace) is a very useful, diagnostic synapomorphy for the most apomorphic genera of Brignoliellini.

A pitted pulmonary plate has developed independently in Brignoliellini (*Pahanga-Borneomma-Brignoliella*), Fallablemmmini, Ablemmmini (*Ablemma*), Tetrablemmmini (*Mariblemma-Shearella-Gunasekara*), and Mattini (*Hexablemma*). The wrinkled surface of the sternum and lateral parts of the carapace in *Gunasekara*, as seen with higher magnification, is an apomorphic modification of the reticulate type. The surface structure of the carapace is fairly variable within many well-defined, large genera (*Brignoliella*, *Tetrablemma*, and *Ablemma*), although some phylogenetically significant trends are present. The marginal area of all pitted Brignoliellini is always coarser than the dorsal part of the cephalic area. The carapace of most species of *Brignoliella* therefore has a serrate margin when viewed dorsally.

The rugosity of all rugose parts in Tetrablemmidae is well correlated with size. Pacullinae, including all large species of this family,

are more rugose than any species of Tetrablemmnae, while all the smallest species (in *Sulaimania*, *Cuangoblemma*, *Monoblemma*, and *Ablemma* s. str.) have a smoother surface of all plates than their larger relatives. Finally, the largest species of *Brignoliella*, *Ablemma*, and *Tetrablemma* are more rugose than small species of the same genera. In a few cases with fairly large variation in size within a single population of a species (*Gunasekara ramboda* and *Brignoliella martensi*), positive allometry of the rugosity can be observed.

Most minor changes in the surface pattern of sclerotized parts are adaptive and as such their phylogenetic value is limited. The detailed patterns of pits in the carapace of some Brignoliellini are a possible and very interesting exception, but too few specimens are known for final assessment of this character as diagnostic at the specific level.

Leg characters

The relative length of legs and position of metatarsal trichobothrium are quite variable in Pacullinae, but almost constant in Tetrablemmnae.

The relative length of legs in *Matta mckenziei* was regarded by Shear (1978: 18) as an adaptation to life in caves. Femur-tarsus/carapace is 2.7 in this species, but 2.74 in males of *M. hambletoni*, although the latter lives in forest litter. Therefore the relative length of legs is rather a generic synapomorphy for *Matta*. The same leg index is between 2.0 and 2.5 in the majority of Tetrablemmnae. There is also a general tendency to group allometry. The relatively longest legs have been measured in large species of *Shearella*, *Gunasekara*, *Brignoliella*, and *Pahanga*. The only species with male leg index below 2.0 are all among the smallest tetrablemmid species measured by myself, and represent four different genera which are not related to each other, viz. *Sulaimania*, *Monoblemma*, *Cuangoblemma*, and *Tetrablemma* (*Kumaonia*). For details, see Table 3 on p. 13.

The relative length of metatarsus and tarsus has been used as a family character for Hadrotarsidae (Hickman 1943, Levi 1968) and

evidently this character is phylogenetically significant in various groups of Araneioidea and related taxa (Araneomorpha sensu Lehtinen, 1978). Until now, the tarsus has most often been known to be longer than the metatarsus in groups with exceptionally tiny species. The same correlation may be true within Tetrablemmnae. The tarsi are distinctly longer than the metatarsi only in tiny species of *Monoblemma*, *Mariblemma*, and *Anansia*.

There are two rows of dorsal tibial trichobothria and one metatarsal dorsal trichobothrium in about position 0.4 in all Tetrablemmnae, and an unpaired tibial trichobothrium distal to the two rows. The position of the tarsal organ and the structure of tarsal claws do not afford any phylogenetically significant diagnostic characters within Tetrablemmnae. For Benoit's (1977) deviating opinions, see p. 59.

Male palpal characters

Tetrablemmnae have a typical haplogyne palpus, and all fairly simple modifications may have occurred more than once.

The relative length of palpal tibia and femur as well as swelling of these segments has been used as a generic (*Cuangoblemma*) or specific character by Brignoli (1974) and Shear (1978, 1979). At least the thickening of palpal tibia, maximally resulting in a rounded posterior process, is a widespread trend among haplogyne groups (Gamasomorphinae, etc.). The relative length and width of all segments of the male palpi can be used in phylogenetic analysis of Tetrablemmnae, if a reservation for possible parallel evolution is taken into account. The most exceptional genera in this respect are *Indicoblemma*, *Pahanga*, *Gunasekara*, and *Cuangoblemma*. A basal, acute cone on the median side of the palpal femur is a practical diagnostic character and synapomorphy for *Tetrablemma* s.str.

The external morphology of the bulbus has been used repeatedly in the compilation of a cladogram for Tetrablemmnae by Shear (1978). However, the shape of the bulbus is easily modified due to slightly different origin of the embolus, thickness and course

of the ejaculatory duct, and possibly to other factors. All main types of bulbi can be found within the large genus *Brignoliella*, and still wider variation within the whole tribe Brignoliellini. Such material was not known to Shear (1978). The origin of the embolus is always the same within a genus of Tetrablemmineae, but externally similar types may have evolved in parallel (*Ablemma* — *Cuangoblemma*, *Mariblemma* — *Singaporemma*).

A basal projection of the embolus is known in three species of *Tetrablemma* s. str. (but not in the type-species) and in *Ablemma* (*Bannia*) *erna*, and a central lamellar widening of the embolus in *Tetrablemma* *alterum*. The whole embolus is strongly modified in all Ablemmiini, and also in *Micromatta* *atoma* and *Gunasekara* *ramboda*.

A conductor is present in all Mattini and regarded as a synapomorphy of this group (Shear 1978). This may be true, but the modifications of the embolic base are topographically different in *Matta*, *Micromatta*, and *Caraimatta*, and if a synapomorphy, it could be more appropriately described as modification of the distal part of the bulbus. A conductor has developed independently three times within Brignoliellini (*Choitroblemma*, *Borneomma* *roberti*, and *Brignoliella* *leletina*).

The course of the ejaculatory duct is not known for all species studied, because single holotype specimens of other museums were not dissected for treatment in lactic acid. It is certain that the course of the ejaculatory duct is not fundamentally different within Tetrablemmineae as it seems to be in many families of Amaurobiomorpha (Lehtinen & Hippa 1979: Lycosidae) and Araneomorpha (Lehtinen & Saaristo 1980: Nesticidae). The ejaculatory duct of Tetrablemmineae usually has one or two circular or transverse, fairly thick basal coils and a distal part that is much narrower, but highly variable in length.

The distal part of the ejaculatory duct is almost straight in Brignoliellini, Fallablemmiini, and Ablemmiini, but usually long and irregularly bent and coiled in all Mattini and most Tetrablemmiini studied by myself or depicted by Shear (1978). The basal coils are very thick and perpendicular to the longitudinal axis in *Tetrablemma* s. str., but more or less obliquely placed in the remaining sub-

genera of *Tetrablemma* as well as in all Ablemmiini studied until now.

The ejaculatory duct usually opens some distance from the apex of the embolus, and there may be minor modifications around this opening, such as a short tooth in *Brignoliella* *martensi*.

Female genital characters

The structures of the female genital organs that are externally visible are traditionally known as epigyne. The structures of this epigynal area in Tetrablemmidae cannot be described in terms of traditional spider taxonomy dealing with families of Amaurobiomorpha or Araneomorpha, and absolutely no homologies between female genital organs of Tetrablemmidae and these two groups can be found as far as organs outside the primary female organs (= ovaria) are concerned. The "epigynal area" of Tetrablemmineae consists of a posterior fold of the pulmonary plate, an unpaired central orifice that is variably bordered by sclerotized margins, and contours of sclerotized parts of the vulva shining through the integument.

Shear (1978) divided Tetrablemmineae into two subfamilies according to position and size of the epigynal pit. I cannot agree with his bifurcate classification of the epigynal pit. The copulatory opening or openings are situated on or behind the pulmonary plate in all other groups of Sicarioidea, including Pacullinae. Thus a posterior site represents the plesiomorphic state of this character in Tetrablemmineae. The plesiomorphic type of embolus has most probably been a thin simple spine. It is therefore assumed also here that the plesiomorphic type of epigynal pit is small or even minute in size. Such a combination of position and size of the epigynal pit is found in at least some species of all tribes of Tetrablemmineae except Ablemmiini, but was unknown to Shear (1978, e.g., for Brignoliellini).

A large epigynal pit is generally correlated with a thick embolus, and such a large pit is usually more anteriorly placed and limited by various sclerotized structures along its margins. A large pit is characteristic for all

Ablemmiini (all with thick, modified embolus), but different types of large pit have also been evolved independently in various evolutionary lines within Brignoliellini and in Fallablemmiini (*Afroblemma*).

The structure of the tetrablemmine vulva is unique among all spider groups that have been analyzed in detail. The soft, paired spermathecae originate from an unpaired copulatory channel that is usually more or less sclerotized and is simply called the vulval stem in this study. An unpaired central process is present in Fallablemmiini, in four plesiomorphic genera of Brignoliellini, in most Tetrablemmiini, and at least in some Mattini, but is certainly absent in all Ablemmiini and in all Brignoliellini with sternal pits. According to this distribution it is obvious that the presence of the central process is a plesiomorphic character in Tetrablemmineae, and that the reduction has occurred several times. The actual reduction in one line of evolution can be followed in the series *Mariblemma* — *Shearella*.

The presence of an inner vulval plate dorsal to the vulval stem and base of the seminal receptacula is shared by all known species of Tetrablemmineae, although the shape of the plesiomorphic type may be disputed. A trifurcate type with narrow central branch is found in Fallablemmiini and most Tetrablemmiini, and thus it is regarded here as the most plesiomorphic type. Another type of trifurcate inner vulval plate is present in all species of *Ablemma*, where the wide, triangular, distally rounded, central branch is fixed to the inner face of the pulmonary plate with distal membranes. A triangular, wide, central branch is also present in *Caraimatta* and in less typical form in its African relative, *Hexablemma*, but obviously not in *Matta*. The most complex inner vulval plates are present in the African genera *Cuangoblemma* and *Anansia*, both regarded here as apomorphic branches of Tetrablemmiini. The central branch is totally reduced at least in the series *Shearella* — *Mariblemma* — *Gunasekara* of Tetrablemmiini, but probably also in some Mattini.

The inner vulval plate of Brignoliellini is very simple in both plesiomorphic and apomorphic genera, and it may be primarily

simple as the central branch is also lacking in all Pacullini. If this is true, Brignoliellini can not be a sister group of Fallablemmiini as supposed here, but rather a plesiomorphic sister group of the rest of Tetrablemmineae (including Fallablemmiini).

The evolution of the vulval stem seems to have been quite different in the five tribes of Tetrablemmineae, although it is still poorly known in Mattini. The simplest and most probably the most plesiomorphic type of vulval stem is found in *Indicoblemma*, *Chavia*, and *Choitroblemma*, all belonging to Brignoliellini. In fact they have only a short unpaired copulatory channel which branches into weakly sclerotized basal parts of the seminal receptacula. The whole central part of the vulva, as well as the basal parts of the paired ducts, has well sclerotized, thick walls in the remaining genera of Brignoliellini, but the sclerotization is generally restricted to these primary structures of the vulva. Only in "*Brignoliella*" *sarawak*, an apomorphic species with unknown affinities, are there more or less well defined anterior ridges in the positions of the lateral horns of Tetrablemmiini. In contrast to other genera of Brignoliellini with reticulate sternum *Singaporemma* has strongly sclerotized basal parts of the vulval ducts, and the dorsal wall of these ducts is distinctly invaginated. Additional apomorphic patterns of sclerotizations of the vulval ducts are present in *Borneomma* and less distinctly in at least some species of *Pahanga*. The seminal receptacula of these species are sclerotized in the basal half. There is no abrupt border between the sclerotized basal parts of the ducts and thin, soft, distal parts of the vulval ducts in these two genera, although the ducts have less sclerotized central parts. The vulval stem of all *Brignoliella* spp. is thick and the sclerotization is equally strong around the unpaired copulatory channel and the abruptly limited short basal part of the paired vulval ducts.

The sclerotization of the central parts of the vulva of all other tribes consists of separate sclerotized structures embracing or supporting the thin, unsclerotized primary vulval ducts ventrally, posteriorly or anteriorly.

It is quite easy to state that the separate ventral plate with long, distally rounded,

lateral extensions in *Fallablemmi* is not homologous with any other supporting structures of the tetrablemmid vulva, and the evolution of all other characters seems to support the hypothesis that *Fallablemma* and *Afroblemma* are not closely related to other recent groups of Tetrablemmiinae. Paired central chitinous strips possibly homologous with the unpaired central process of other genera fix the vulval stem of *Fallablemma* to the inner surface of the pulmonary plate.

The central vulval stem is exceptionally wide in *Hexablemma* and *Caratmatta*, suggesting a relationship between these geographically distant genera. Their relationship with *Matta* and inclusion in Mattini is argued mainly with male characters. The central parts of the vulva also deviate in *Anansia* and "*Monoblemma muchmorei*", and a cladistic arrangement of the Tetrablemmi-Mattini complex remains somewhat uncertain. However, the limitation of the whole complex poses no difficulties, except possibly concerning the inclusion or exclusion of the genus *Matijana*.

The derivation of the tetrablemmine vulva from that of other Sicarioidea is not easy, even with reference to the vulva of Pacullinae. The copulatory orifice of Pacullinae is always behind the pulmonary plate, and the homology of the single, large vulval plate of Pacullinae with tetrablemmine vulval structures remains somewhat uncertain. It may be the same as the inner vulval plate that is present in all tetrablemmine species as a separate plate, but there are other alternatives, too. The position of the soft vulval ducts is known exactly only in the paculline genus *Lamania* where the pattern seems to be the same as in the plesiomorphic type of Tetrablemmiinae (*Indicoblemma*, etc.).

Brignoli (1974) regarded the central vulval process of Tetrablemmiinae as an unpaired seminal receptaculum, while he called the soft paired sacks "posterior seminal receptacula" analogous to structures generally known to occur in Oonopoidea (Oonopidae, Dysderidae, Segestriidae). Shear (1978) presented several drawings with the central process, but he did not name it or discuss its function or homologies. He did not know of the deviating type of vulval stem of Mattini. Thus the vulva of *Caratmatta cambridgei* was

depicted as quite similar to the vulvae of *Tetrablemma*.

The inner vulval plate was regarded as a posterior stigma by Brignoli (1974: 181), but Shear (1978) correctly stated that the posterior stigma is present as an insignificant knob on the inner surface of the preanal plate.

Cooke (1966: fig. 3) described a sclerotized inner plate in the vulva of *Dysdera* and called it the "median entochondrite of the genital somite". This structure may be partly homologous with the inner vulval plate of Tetrablemmiinae and/or the vulval plate of Pacullinae.

Soft spermathecae are known in at least Palpimanidae (Platnick, 1975) and Diguettidae (Gertsch, 1958a) and they probably represent the plesiomorphic character state in both Sicarioidea and Oonopoidea. An unpaired, central, anterior "spermatheca" is present in all Oonopoidea studied in detail. A description of such a vulva has been presented by Cooke (1966) for Dysderidae and by Beatty (1970) for Segestriidae (*Ariadna*). Brignoli (1975) discussed the homology of haplogyne vulvae of different families and he also compared the diguetid vulva with anterior unpaired spermatheca to the tetrablemmine vulva.

A comparative study of the vulvae of different Ochyroceratid genera (Lehtinen unpublished) has revealed that the shape, pattern and degree of sclerotization of spermathecae is quite variable within this well-limited family of Sicarioidea.

The sclerotization of soft spermathecae has most probably taken place in various lines of the evolution of the haplogyne spiders, and most probably also more than once within Sicarioidea. In my opinion, the combination of an unpaired vulval structure (spermatheca, gland, etc.) and paired soft spermathecae represents a very old, plesiomorphic type. The development of a separate, posterior spermatheca in Oonopoidea could be a later synapomorphy for this group and the sclerotization of paired spermatheca in Loxoscelidae, Sicariidae, etc. a synapomorphy for this group within Sicarioidea, but only convergence when compared with sclerotized spermatheca in Filistatidae, Theraphosoidea, Ctenizoidea, and other primitive groups of spiders.

The soft unpaired bursa copulatrix of

Diguettidae (Gertsch 1958) is probably homologous with the paired seminal receptacula of Tetrablemmidae, and the "unpaired seminal receptaculum" of Diguettidae is simply the central process of Tetrablemmidae. It is difficult to understand that such a small structure could act as a receptaculum in any family, and it most probably has similar (secretory?) functions in Diguettidae and primitive Tetrablemmidae (*Afroblemma*, etc.).

Although the vulval structure of Tetrablemmiinae or Pacullinae is not very similar to that of any other group of Sicarioidea it is quite possible that Diguettidae could be the closest recent relative of Tetrablemmidae. This suggestion is supported by similar trends in sexual dimorphism of Tetrablemmidae and various undescribed Neotropical species of Diguettidae (unpaired clypeal horn, sclerotized abdomen with several plates, etc.).

The vulval structure of Tetrablemmidae or that of any haplogyne family cannot be compared with the vulvae of Araneomorpha and Amaurobiomorpha, and any similarity between haplogyne spiders and these two lines of spider evolution are due to convergence in the strive towards an essentially better degree of organization (Lehtinen 1978). Forster (1980) has recently presented a review of the vulval structure of various primitive groups (= spiders definitively belonging outside my Araneomorpha and Amaurobiomorpha). His findings seem to support the hypothesis that the vulvae of haplogyne, hypochiloid, mecysmauchenid, and some other enigmatic groups of spiders cannot be derived from anything present in Amaurobiomorpha or Araneomorpha or vice versa. The vulvae of Theraphosomorph groups are similar to many vulvae in Sicarioidea (Sicariidae), but also to those of Filistatidae, Hypochilidae, etc. This similarity may be simply symplesiomorphy, but it does not deny a phylogenetic relationship between Sicarioidea and Theraphosomorpha as suggested by the author (Lehtinen 1978). On the other hand, there are no synapomorphies or even symplesiomorphies between the complex genital organs of the "haplogyne" spiders and Araneomorpha or Amaurobiomorpha. As emphasized earlier (Lehtinen 1978) the suggested synapomorphies of other characters are either structurally

simple and thus easily acquired by convergence (gnathocoxal serrula), parallel reductions (number and pattern of spinnerets), or only similar in appearance, but not identical in detail (chelicerae). Forster (1980) has shown convincing differences in the structure of the tarsal organ.

The phylogenetic position of Tetrablemmidae within Sicarioidea and that of Sicarioidea within the order Araneae cannot be finally solved yet, but recent strong interest in the haplogyne spiders by various arachnologists will probably solve most of the main problems in the near future.

The cladogram of Tetrablemmidae is based on the analysis of evolution presented here. As stated above, the polarity of evolution of some characters is not absolutely proven (vulval characters, male cheliceral modifications). However, a lot of characters used seem to be phylogenetically quite reliable, and possible alterations due to later information about new taxa mostly seem to affect the cladistics of the tribes, and not their delimitation with regard to known taxa.

Information about the evolution of all characters discussed here is used in determining the phylogenetic relationship between all branches of the cladogram, but for purely practical reasons only a few synapomorphies are actually depicted. The most uncertain points (*Matijana* and *Monoblemma*) are shown by dotted lines. Some genera which are known by one sex only (*Hexablemma*, *Sulaimania*, *Singalangia*, *Rhinoblemma*) could not be characterized with apomorphies of the other sex, although their comparison with related genera would probably be easier if characters of both sexes could be included.

The evolution of Tetrablemmidae is very complex, and several trends are certainly present in addition to generally accepted synapomorphies. The treatment of these trends according to the strict principles of Hennigian taxonomy is impossible. A totally Hennigian cladogram based on absolutely proved synapomorphies at each branching point can in no way be constructed with the information available now, although Shear (1978) did try. In my opinion the most important principle of phylogenetic taxonomy still consists of simultaneous use of all inter-

Cladogram of tetrablemmid genera

Circle = plesiomorphic state of character
 Square = apomorphic state of character
 Capital letters refer to characters listed below and letters of lower case indicate the alternative of apomorphy. Squares with both symbols identical refer to cases of convergent evolution.
 Dotted lines refer to uncertain position of corresponding genera.

List of characters and their apomorphic states

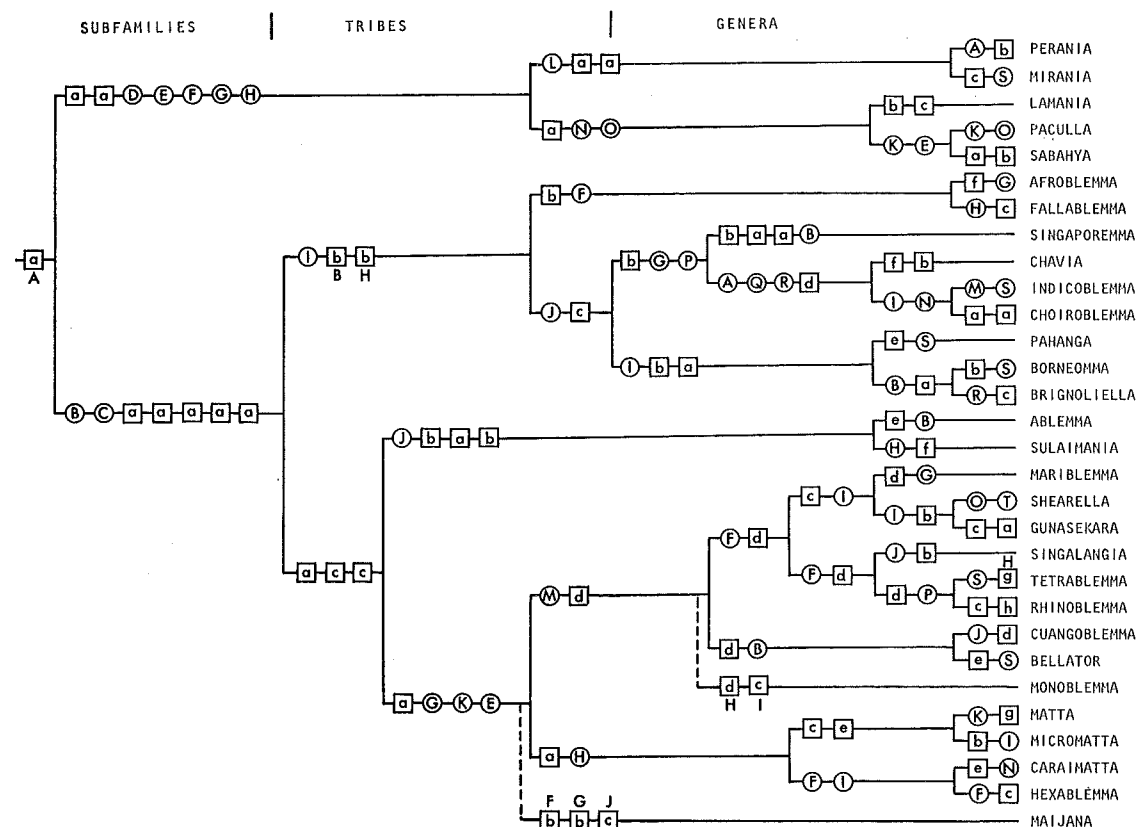
- A. lateral abdominal scuta
 a) present
 b) plate I totally reduced
 c) male plates posteriorly branched
- B. postgenital and preanal plates
 a) male postgenital plate reduced in size
 b) central pits present in the preanal plate
 c) postgenital plate laterally broken to perigenital plates
 d) postgenital plate shortened
 e) preanal plate with other than central paired grooves
 f) postgenital and preanal plates subequal in size
- C. structure of hair pits of carapace and sternum
 a) small or minute
- D. total size of the spider
 a) small or minute
- D. epigynal orifice
 a) minute and unpaired
 b) secondarily large, moved anteriorly
 c) unpaired
- F. structure of the inner vulval plate
 a) separate from other vulval sclerotizations, trifurcate
 b) central branch short and wide, semicircular
 c) central branch totally reduced
 d) lateral branches with anterior modifications
 e) central branch triangular, basally wide
- G. central process of vulva
 a) present
 b) secondarily reduced
 c) modified to bifurcate chitinous strip
- H. male cheliceral modifications
 a) modifications present on the anterior face
 b) sublateral small tooth
 c) other types of anterior modifications (further evolution unclear)
 d) basally wide horn
 e) distal tooth
- f) whole chelicerae wide, divergent
 g) cheliceral horn curved backwards
 h) cheliceral horn curved inwards
- I. eye pattern
 a) compact (ALE close to each other, PME behind ALE)
 b) ocular area narrowed
 c) ALE fused together
 d) eyes reduced to four (PME absent)
 e) eyes reduced to two (PLE absent)
 f) one row of six closely spaced eyes
 g) ALE secondarily far from each other
- J. structure of the vulval stem
 a) copulatory channel sclerotized
 b) ventral separate plate with rounded lateral branches
 c) lateral horns very long
 d) lateral horns posteriorly supporting the vulval ducts
 e) anterior horns with convex anterior margin
- K. structure of embolus
 a) embolic base modified
 b) embolus short and wide
- L. shape of cymbium
 a) shortened, apex bilobate
- M. conductor
 a) present
- N. structure of the pulmonary plate
 a) separate stigmal plates
 b) strongly pitted surface
 c) epigynal fold with a central groove
- O. modifications of leg I in male
 a) metatarsal and tibial cusps (modified bases of short spines) present
 b) metatarsal and tibial irregular spines present
 c) metatarsi strongly modified
- P. sternal characters
 a) surface pitted
 b) posterior part of sternum strongly modified
- Q. origination of embolus
 a) mesial (plesiomorphic: distal)
- R. sclerotization of vulval ducts
 a) basal parts strongly sclerotized and anteriorly modified
 b) seminal receptacula partly sclerotized
- S. male clypeal modifications
 a) male clypeus modified
 b) unpaired tooth on the ventral margin
 c) central (primarily paired) clypeal horn
 d) paired teeth immediately below the eyes
- T. male gnathocoxae
 a) modified

pretable characters. If the evolution of some characters does not fit into the Hennigian scheme compiled according to selected characters, we cannot simply ignore them or make a hypothesis of oscillating evolution of complex structures.

If the compact eye pattern of Ablemmi, Tetrablemmi, and Mattini is regarded as a proven synapomorphy, the vulval structure

strongly suggests that Ablemmi is a sister group of Tetrablemmi-Mattini.

The central part of the vulva of Ablemmi is entirely different from all other types of tetrablemmine vulvae, and even the homologization of its parts cause some difficulties. The epigynal orifice has been removed far from the margin of the pulmonary plate, and there is actually no unpaired copulatory chan-



nel at all, but the soft vulval ducts originate directly from the lateral margins of the large epigynal pit. The sclerotized structures of the central vulval area consist of a well-developed, folded plate anterior to the epigynal pit and well-sclerotized folded margins of the epigynal pit embracing the base of the soft vulval ducts. The area strictly taken as homologous with the vulval stem of other Tetrablemmi, i.e. inside of the posterior part of the pulmonary plate between its posterior margin and the epigynal orifice, has been variably modified in different species or species groups of *Ablemma*, but the homology of this region with the vulval stem of other tribes is proven by the similar fixation of the base of the inner vulval plate.

Even in the situation that the synapomorphy of the compact eye group of Ablemmi, Tetrablemmi, and Mattini is not accepted, a direct comparison of the vulvae of Ablem-

mini and Brignoliellini is impossible, and in my opinion the transfer of the epigynal pit in some (but not all) Brignoliellini and Ablemmi to an exceptional anterior position is due to convergence only. Fallablemmi and Ablemmi both have a well developed inner vulval plate (as do all plesiomorphic Tetrablemmi and Mattini), but these two tribes have practically nothing else in common, and the large inner vulval plate is most probably a symplesiomorphic character. Thus only a loose phylogenetic relationship with Tetrablemmi and Mattini seems to remain for the enigmatic, but locally very successful group of Ablemmi.

The vulval stem of most Tetrablemmi consists of a strongly sclerotized central part and paired lateral tapering horns which usually support the base of the soft vulval ducts posteriorly. The vulva of *Matta* is not very different at first sight, but in fact its lateral

horns do not posteriorly support the vulval ducts, but embrace the entire basal parts of the ducts as do the laterally unextended sclerotizations of Brignoliellini.

5. Zoogeography

Shear (1978:6) emphasized the position of Southeast Asia as the centre of diversity for Tetrablemmidae. I totally agree with him in this respect, although his more detailed zoogeographical conclusions seem to be wrong, mainly because he discussed the distribution of polyphyletic taxa (Brignoliellinae, Tetrablemmineae sensu Shear, *Monoblemma* sensu Shear). The tetrablemmid fauna of Africa is still very imperfectly known, but it may be almost as rich in species as any part of the Indo-Pacific area. The actual difference in the number of species as well as specimens between the Indo-Pacific and the South American areas is well demonstrated by the tetrablemmid specimens which I collected during recent expeditions to these areas and during which I used the same methods. Tetrablemmids were also among the particular families that were searched for in both areas. My two expeditions to northwestern South America and the West Indies yielded not a single specimen of Tetrablemmidae, while six expeditions of approximately similar duration to the Indo-Pacific area resulted in well over 2000 specimens of tetrablemmids, representing 52 named species and all main areas of collection.

The range of the subfamily Pacullinae is most probably restricted to the Oriental region, and additional species are mainly to be awaited from the areas in which the majority of the species have been found until now. The two tribes, Peranilini and Pacullini are largely sympatric.

The distribution of Tetrablemmineae is best discussed with reference to the tribes. The only exception is the genus *Tetrablemma* which certainly has an exceptional capacity for dispersal and consequently an exceptionally wide range over whole of the Old World.

Many of its species live under the bark of trees and they can therefore be easily dispersed with floating timber and, at least in exceptional cases, by zoochorous or even anthropochorous dispersal (*T. extorris* — cf. Shear 1978:7). The origin of Tetrablemmineae is best determined with the aid of other genera. *Singalangia* and *Rhinoblemma*, the closest relatives of *Tetrablemma*, live in the eastern half of the Indo-Pacific area, and at least this subtribe seems to originate from the centre of diversity of Tetrablemmidae. Another group of related genera, *Shearella*—*Mariblemma*—*Gunasekara*, is only known from islands in the Indian Ocean. A few genera of Tetrablemmineae are known from the Ethiopian region, but their phylogenetic relationship to the two above-mentioned subgroups dominating in the Indo-Pacific region is not very close. However, this distribution of the different subgroups of Tetrablemmineae seems to prove that ancestors of these subgroups were present in different parts of the Gondwana during the first half of the Mesozoic era. Ancestors of Mattini probably lived in the united ancient block of South America and Africa and they were evolved to different genera since the separation of these continents.

The known range of Ablemmineae is almost identical to that of Pacullinae and also to the centre of diversity of the whole family.

The present distribution of Brignoliellini fits very well into the suggested phylogenetic relationships of its genera. All primitive genera with reticulate sternum (*Indicoblemma*, *Chavia*, *Choirobemma*, and *Singaporemma*) are restricted to the continental parts of the Oriental region, while the centre of diversity for the three genera with pitted sternum (*Borneomma*, *Pahanga*, and *Brignoliella*) is more eastern, and again identical to the centre of diversity of the whole family.

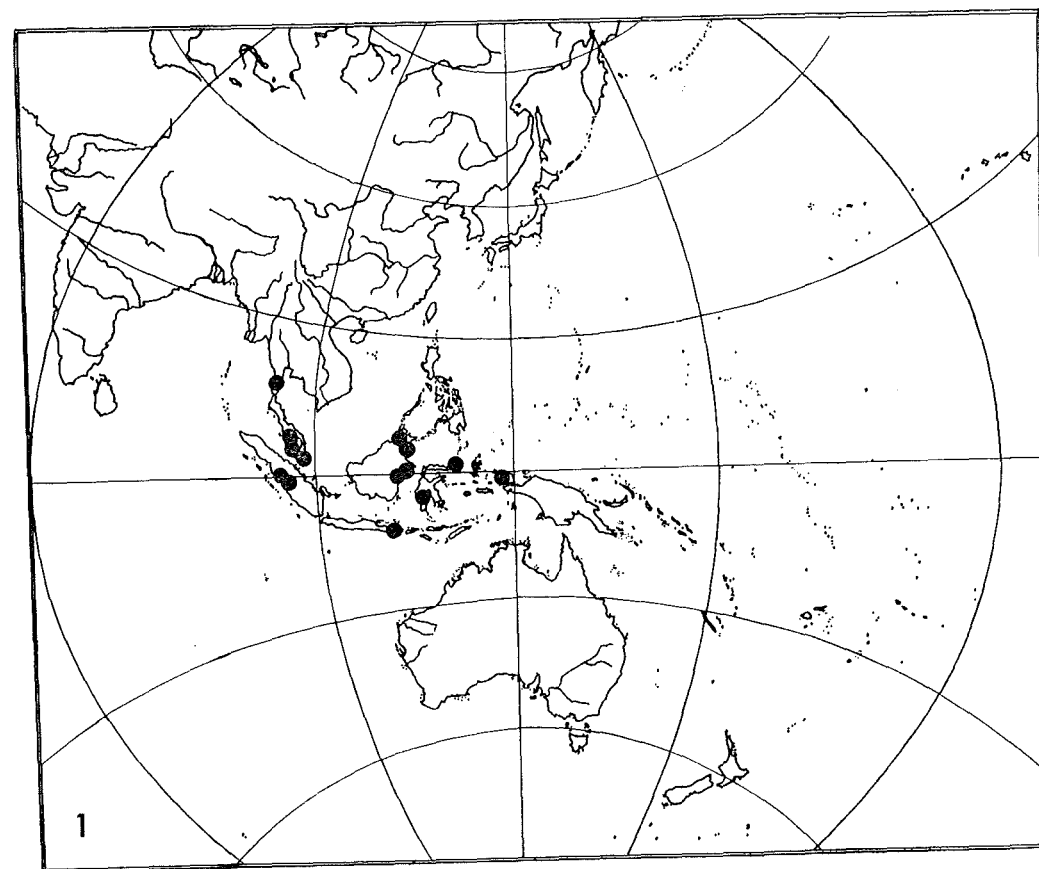
However, no representatives of the former group are known from peninsular India, and thus the origin of Brignoliellini may be in the mountain region of continental Southeast Asia (Southern China to Malaya).

The most interesting tribe of Tetrablemmineae from a purely zoogeographical viewpoint is Fallablemmineae. Although species of Fallablemmineae are ecologically quite similar to Brignoliellini, they have been distributed from West Africa to Samoa. This seems to prove that Fallablemmineae is older than Brignoliellini and most subgroups of Tetrablemmineae, all of which have a more limited total range, but show more intensive speciation during the Cenozoic era.

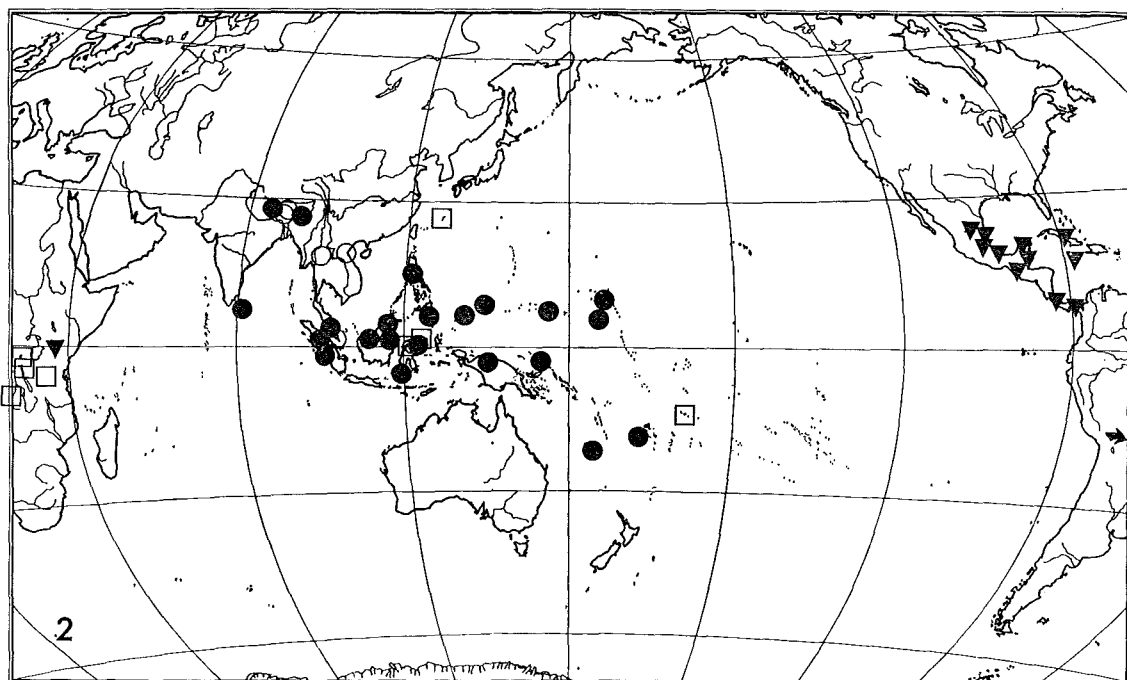
The known distribution of Tetrablemmidae (Maps 1—3) suggests that their ancestors were southeastern Laurasian. However, ancestors of Tetrablemmineae and Mattini were widely distributed

in northern Gondwana (land mass of Africa and South America) some 180 million years ago, before the separation of Africa and South America, but recent genera of both of these tribes have evolved later. The presence of the genus *Afroblemma* in tropical Africa may be best explained by the wide range of Fallablemmineae in the middle of the Cenozoic era and the subsequent extinction of this group in the wide gap between known ranges of *Fallablemma* and *Afroblemma*. The presence of some rare species of Fallablemmineae in this area is naturally possible, as the ground-living spider fauna of tropical continental Asia is not too well-known.

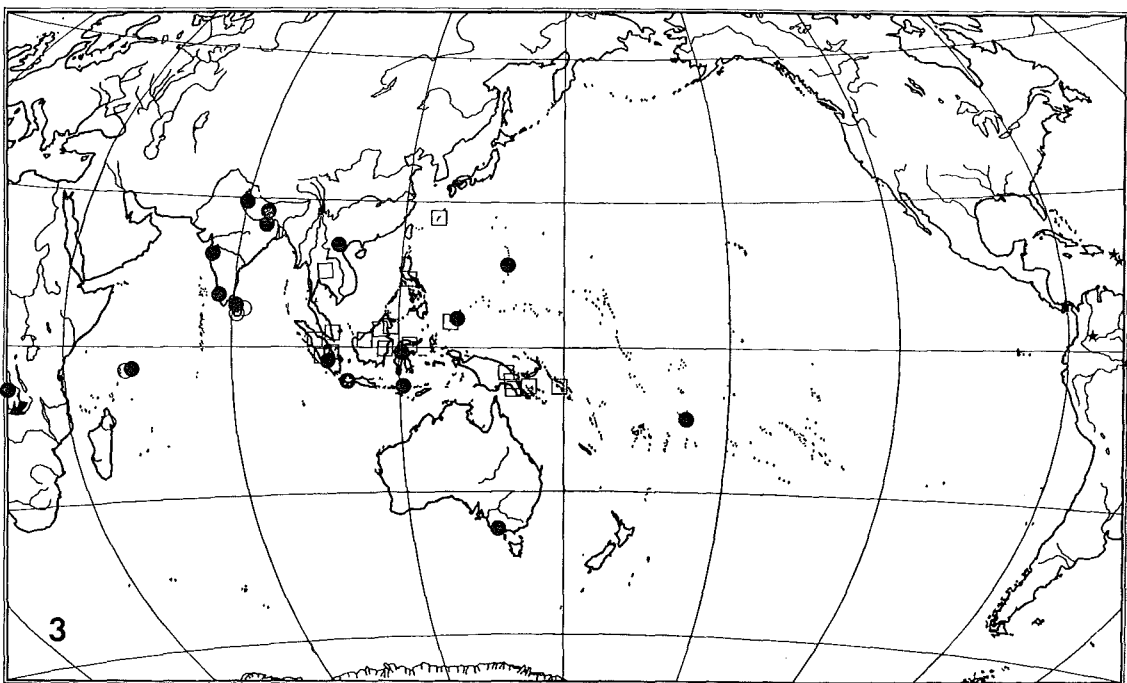
Tetrablemmids have probably never existed in the southern parts of Gondwana, represented now by southern South America, New Zealand, Tasmania, South Africa, etc. The long union of the land masses of southern



Map 1. Distribution of Pacullinae.



Map 2. Distribution of Fallablemmiini (open squares), Brignoliellini (open circles: species with reticulate sternum; filled circles: species with pitted sternum), and Mattini (filled triangles).



Map 3. Distribution of Ablemmiini (open squares), Tetrablemmiini (open circles: *Mariblemma-Shearella-Gunasekara*; filled circles: *Singalania-Tetrablemma-Rhinoblemma*; black stars: *Monoblemma* & "*Monoblemma*"; black points to range of *Cuangoblemma-Anansia* outside the map), and *Maijana* (circle with star). The range of the genus *Tetrablemma* extends outside the map into both directions.

Gondwana has most probably played no part in the zoogeography of Tetrablemmidae, and even then only known southern Australian species *Tetrablemma okei* belongs to the easily spread species which live under the bark of trees. The nearest relatives of this species live in India and western Africa.

The definitely monophyletic group *Mari-blemma-Shearella-Gunasekara* includes the only six-eyed species of Tetrablemmiini, and its evolution may have long been continued in total isolation from other groups of Tetrablemmiini. However, the origin of this group with its recent range in islands of the Indian ocean can hardly be southern Gondwanian. It may have originated from Africa and later changed its main area towards the east. Besides, the African tetrablemmid fauna is far more poorly known than that of Asia or the northern part of the Neotropical region, and species of this subtribe of Tetrablemmiini may well live in continental Africa.

Only species of the genus *Tetrablemma* are known from peninsular India, and all the species on the southern slopes of the Himalayas seem to have penetrated there from the east. Therefore it is possible that the separate Indian plate had no tetrablemmids before its collision with the northern shore of the Tethys Sea.

No tetrablemmid fossils are known from Baltic amber or other Laurasian sites, in contrast to some other groups of spiders now restricted to the more southern, tropical area (Archaeidae, Cyatholipidae: *Viocurus*). For details, see Petrunkevitch (1958). Tetrablemmids constitute an excellent group for study of vicariance zoogeography because their dispersal is usually very slow.

Abbreviations

Museums:

- AMNH = American Museum of Natural History, New York
 BBM = Bernice P. Bishop Museum, Honolulu
 BMNH = British Museum, Natural History, London
 CNC = Canadian National Collection, Ottawa
 DEUP = Department of Entomology, The University of the Philippines, Los Baños
 HDE = Hope Department of Entomology, Oxford

- FMNH = Field Museum of Natural History, Chicago
 IZR = Istituto di Zoologia, Università di Roma, Roma
 LNK = Landessammlungen für Naturkunde, Karlsruhe
 NMM = National Museum, Melbourne
 NMNH = National Museum of Natural History, Smithsonian Institution, Washington
 MCSN = Museo Civico di Storia Naturale "Giacomo Doria", Genoa
 MCZ = Museum of Comparative Zoology, Harvard University, Cambridge, Mass.
 MD = Museu do Dundo, Dundo
 MNHG = Muséum d'Histoire Naturelle, Geneva
 MNHN = Muséum National d'Histoire Naturelle, Paris
 MRAC = Musée Royal de L'Afrique Centrale, Tervuren
 MZT = Zoological Museum, Department of Biology, University of Turku, Turku
 RMNH = Rijksmuseum van Natuurlijke Historie, Leiden
 SMF = Senckenberg-Museum, Frankfurt am Main
 ZMC = Zoologiske Museum, Copenhagen
 ZMH = Zoologisches Museum der Universität Hamburg, Hamburg
 ZSI = Zoological Survey of India, Calcutta/Poona

Collector:

- PTL = Pekka T. Lehtinen

Morphology:

- ALE = anterior lateral eyes
 PLE = posterior lateral eyes
 PME = posterior median eyes
 Tmt I = trichobothrium on metatarsus I

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Checklist of Tetrablemmidae

Pacullinae Simon, 1893

PM MZT

Peranilini

<i>Perania nigra</i> (Thorell, 1890) = <i>P. pallida</i> Thorell, 1890	Sumatra	♂♀
<i>P. picea</i> (Thorell, 1890) = <i>P. korinchica</i> Hogg, 1920	Sumatra	♂♀
<i>P. birmanica</i> (Thorell, 1898)	S Burma	♀
<i>Mirania armata</i> (Thorell, 1890)	Sumatra	♀ ♂

Pacullini

<i>Paculla granulosa</i> (Thorell, 1881)	W New Guinea	♂
<i>P. sulaimani</i> n. sp.	Malaya	♂
<i>P. negara</i> Shear, 1978	Malaya	♂ ♀
<i>Lamania nirmala</i> n. sp.	E Borneo	♂♀
<i>L. bernhardi</i> (Deeleman-Reinhold, 1980)	E Borneo	♂♀ ♀
<i>L. kraui</i> (Shear, 1978)	Malaya	♂♀
<i>L. inornata</i> (Deeleman-Reinhold, 1980)	N Borneo	♂♀
<i>L. sheari</i> (Brignoli, 1980)	S Celebes	♂
<i>Sabahya kinabaluana</i> Deeleman-Reinhold, 1980	N Borneo	♂♀ ♂♀
<i>S. bispinosa</i> Deeleman-Reinhold, 1980	N Borneo	♀
" <i>Paculla</i> " <i>cameronensis</i> Shear, 1978	Malaya	♂

Tetrablemmiinae O. Pickard-Cambridge, 1873

Fallablemmiini

<i>Afroblemma t. thorelli</i> (Brignoli, 1974)	Angola	♂♀
<i>A. t. maniema</i> n. ssp.	Zaire	♂♀
<i>Fallablemma castaneum</i> (Marples, 1955)	Samoa	♂♀
<i>F. greeni</i> n. sp.	N Celebes	♂♀

Brignoliellini

<i>Indicoblemma sheari</i> Bourne, 1980	E Himalaya	♂♀ ♂♀
<i>Chavia monticola</i> n. sp.	N Thailand	♀
<i>Choiroblemma bengalense</i> Bourne, 1980	E Himalaya	♂♀
<i>C. rhinoxunum</i> Bourne, 1980	E Himalaya	♂♀
<i>Singaporemma singularis</i> Shear, 1978	Singapore	♂♀
<i>S. halongensis</i> n. sp.	N Vietnam	♂♀
<i>S. adjacens</i> n. sp.	N Vietnam	♂♀
<i>Pahanga dura</i> Shear, 1979	Malaya	♂
<i>P. lilisari</i> n. sp.	Sumatra	♂♀
<i>P. diyaluma</i> n. sp.	Ceylon	♀
<i>P. centennialis</i> n. sp.	Malaya	♀
<i>Borneomma</i> (B.) <i>roberti</i> Deeleman-Reinhold, 1980	N Borneo	♂♀ ♂
<i>B. (Oleoblemma) yuata</i> n. sp.	E Borneo	♂♀
<i>Brignoliella</i> (B.) <i>acuminata</i> Simon, 1889	New Caledonia	♀ ♂♀
<i>B. (B.) vitiensis</i> n. sp.	Fiji	♀
<i>B. (B.) beattyi</i> Shear, 1978	Caroline Isl	♂♀
<i>B. (B.) dankobiensis</i> Bourne, 1980	New Ireland	♂
<i>B. (B.) trifida</i> n. sp.	E Borneo	♂
<i>B. (B.) delphina</i> Deeleman-Reinhold, 1980	W New Guinea	♂♀
<i>B. (B.) carmen</i> n. sp.	Mindanao	♂♀
<i>B. (B.) bicornis</i> (Simon, 1893)	Luzon	♂♀ ♀
<i>B. (B.) quadricornis</i> (Roewer, 1963)	Caroline Isl.	♂♀
<i>B. (B.) martensi</i> (Brignoli, 1972)	C Himalaya	♀ ♂♀
<i>B. (B.) besuchetiana</i> Bourne, 1980	Assam	♂♀
<i>B. (B.) vulgaris</i> n. sp.	N Borneo	♂♀
<i>B. (B.) maros</i> n. sp.	S Celebes	♂♀
<i>B. (B.) klabati</i> n. sp.	N Celebes	♀
<i>B. (B.) massai</i> n. sp.	N Celebes	♂♀
<i>B. (Ceratoblemma) michaeli</i> n. sp.	Malaya	♂♀
<i>B. (C.) scrobiculata</i> (Simon, 1893)	Ceylon	♀
<i>B. (Diploblemma) leletina</i> Bourne, 1980	New Ireland	♂
" <i>Brignoliella</i> " <i>sarawak</i> Shear, 1978	W Borneo	♀

Ablemmi		PM	MZT
Ablemma (Ablemma) baso Roewer, 1963	Sumatra	♂♀	
A. (A.) sternofoveata n. sp.	E Borneo		♀
A. (A.) shimojanai (Komatsu, 1968)	Ryukyu Islands	♂♀	
A. (A.) berryi Shear, 1978	Caroline Islands	♂♀	
A. (Bannia) k. kaindi n. sp.	E New Guinea		♂♀
A. (B.) k. avios n. ssp.	E New Guinea		♂♀
A. (B.) circumspectans Deeleman-Reinhold, 1980	N Borneo	♂♀	♂♀
A. (B.) merotai n. sp.	E Borneo		♂
A. (B.) lempake n. sp.	E Borneo		♂♀
A. (B.) samarinda n. sp.	E Borneo		♂
A. (B.) sedgwicki Shear, 1978	W Borneo	♂	
A. (B.) singalang n. sp.	Sumatra		♂
A. (B.) datahu n. sp.	N Celebes		♂♀
A. (B.) rarosae n. sp.	Luzon		♂
A. (B.) alyura Shear, 1978	E New Guinea	♂♀	
A. (B.) erna n. sp.	Sumatra		♂♀
A. (B.) girinum n. sp.	E New Guinea		♂
A. (B.) pugnax (Brignoli, 1973)	Solomon Sea Islands	♀	♀
A. (B.) syahdani n. sp.	E Borneo		♀
A. (B.) ruohomaekii n. sp.	C Thailand		♂♀
A. (B.) makiling n. sp.	Luzon		♂♀
Sulaimania vigelandi n. sp.	Malaya		♂
Tetrablemmi			
Mariblemma pandani (Brignoli, 1978)	Seychelle Islands	♂♀	
Shearella lilawati n. sp.	Ceylon		♂♀
S. selvarani n. sp.	Ceylon		♂♀
S. browni (Shear, 1978)	Madagascar	♂	
Gunasekara ramboda n. sp.	Ceylon		♂♀
Singalangia sternalis n. sp.	Sumatra		♀
Tetrablemma (Kumaonia) loebli Bourne, 1980	W Himalaya	♂♀	♂♀
T. (Indonops) deccanensis (Tikader, 1975)	W India	♂♀	♂♀
T. (I.) samoensis Marples, 1964	Samoa	♂♀	
T. (I.) viduum (Brignoli, 1974)	Angola	♀	
T. (I.) helenensis Benoit, 1977	St Helena	♀	
T. (I.) benoitii (Brignoli, 1978)	Seychelle Islands	♀	
T. (I.) marawula n. sp.	C Celebes		♂♀
T. (I.) mardionoi n. sp.	Sumatra		♂♀
T. (I.) manggarai n. sp.	Flores		♂♀
T. (I.) vietnamensis n. sp.	N Vietnam		♀
T. (I.) phulchoki n. sp.	C Himalaya		♀
T. (? I.) alterum Roewer, 1963	Mariana Islands	♂♀	
T. (Tetrablemma) m. medioculatum O. Pickard-Cambridge, 1873	Ceylon	♂	
T. (T.) m. gangeticum n. ssp.	N India		♂♀
T. (T.) m. cochinese n. ssp.	S India		♂♀
T. (T.) extorris Shear, 1978	? Trinidad	♂	
T. (T.) rhinoceros (Brignoli, 1974)	Angola	♂♀	
T. (T.) brignolii n. sp.	S India		♂♀
T. (T.) okei Butler, 1932	SE Australia	♀	♂♀
Rhinoblemma unicornis (Roewer, 1963)	Caroline Islands	♂♀	
Cuangoblemma machadoi Brignoli, 1974	Angola	♂♀	
Anansia astaroth (Brignoli, 1974)	Angola	♂♀	
Mattini			
Matta hambletoni Crosby, 1934	SE Brazil	♂♀	
M. mckenziei Shear, 1978	Mexico	♂♀	
Micromatta atoma (Shear, 1978)	Belize	♂♀	
Caralmatta sbordonii (Brignoli, 1972)	Mexico	♂♀	
C. blandini n. sp.	Mexico		♀
C. cambridgei (Bryant, 1940)	Cuba - Jamaica	♂♀	
Hexablemma cataphractum Berland, 1920	Kenya		♀

Incertae sedis

Monoblemma unicum Gertsch, 1941
 "Monoblemma" muchmorei Shear, 1978
 "Monoblemma" becki Brignoli, 1978
 Maijana racki n. sp.

PM MZT
 Panama ♂
 Virgin Islands ♂♀
 Amazon region ♀
 Java ♀

PM = published material (deposition variable)
 MZT = previously unpublished material in MZT

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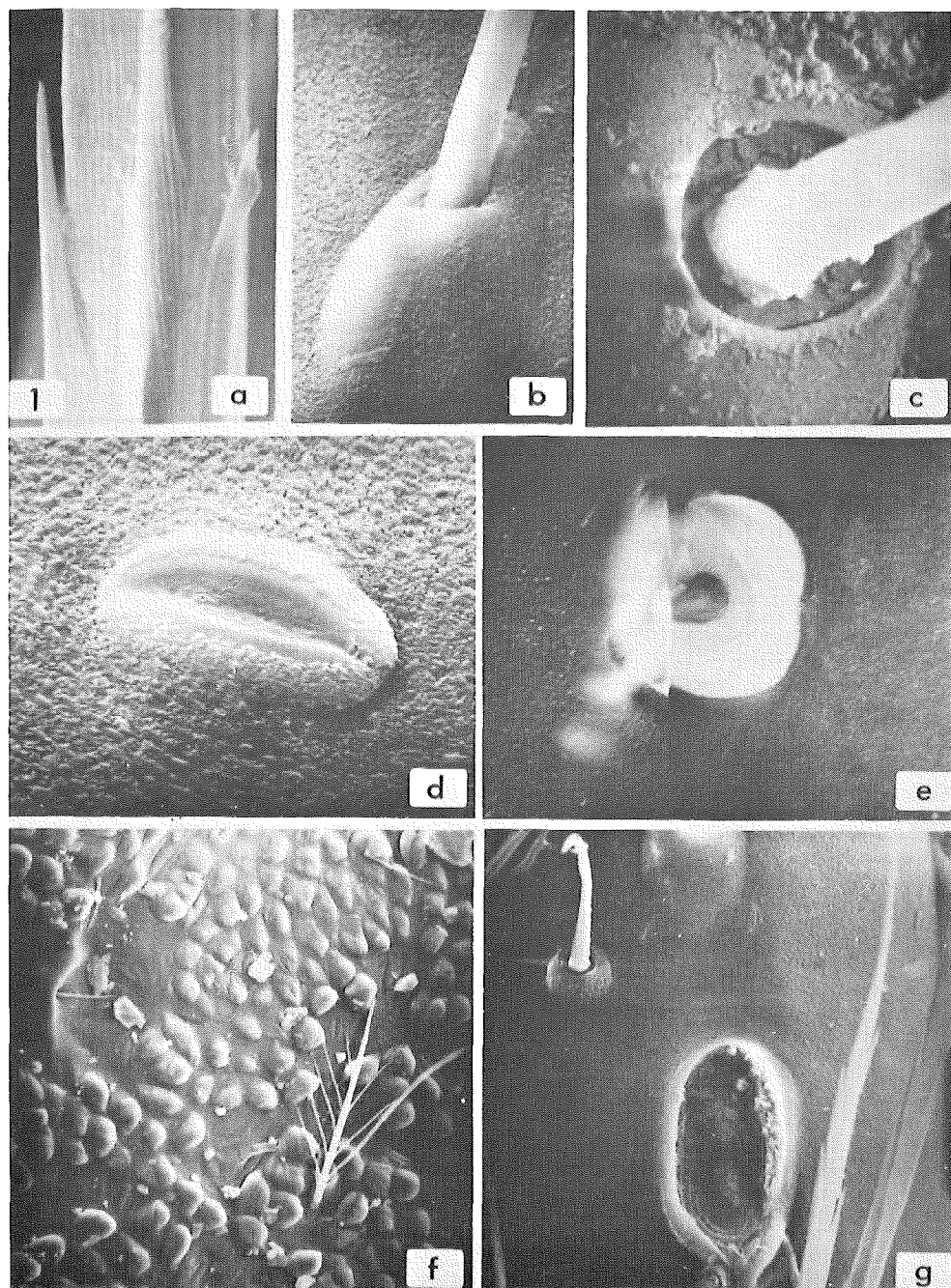


Fig. 1 a—g: Ultrastructure of Tetrablemmidae Pacullinae, *Sabahya kinabaluana* Deeleman-Reinhold. — a: tarsal hair $\times 7000$. — b: base of tibial hair $\times 3000$. — c: base of minute hair from tibial base $\times 10\,000$. — d: slit sense organ from tibial surface $\times 6000$. — e: base of tibial trichobothrium $\times 2000$. — f: surface and hair types of carapace $\times 600$. — g: tarsal organ and sensory hair $\times 1600$.

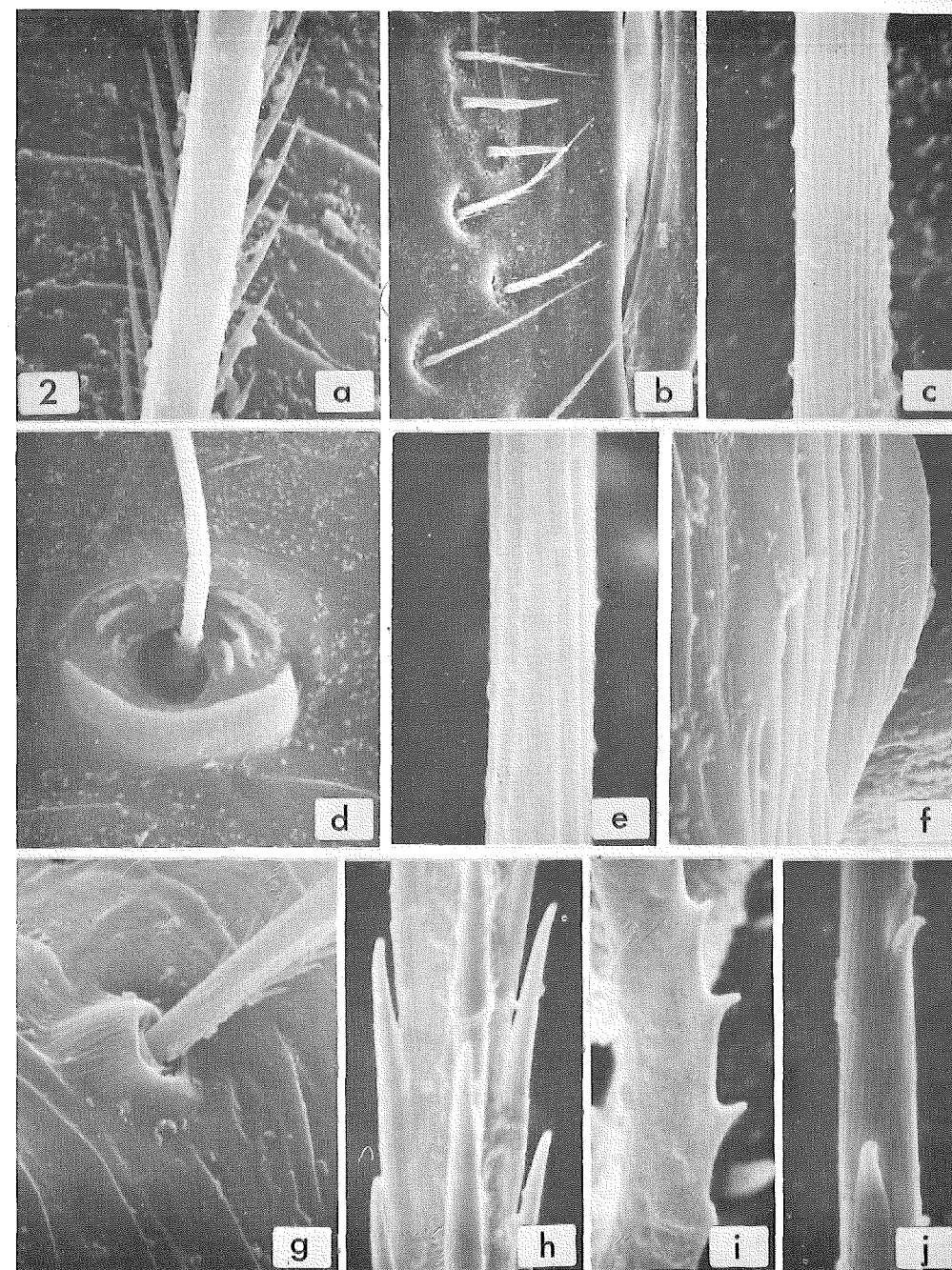
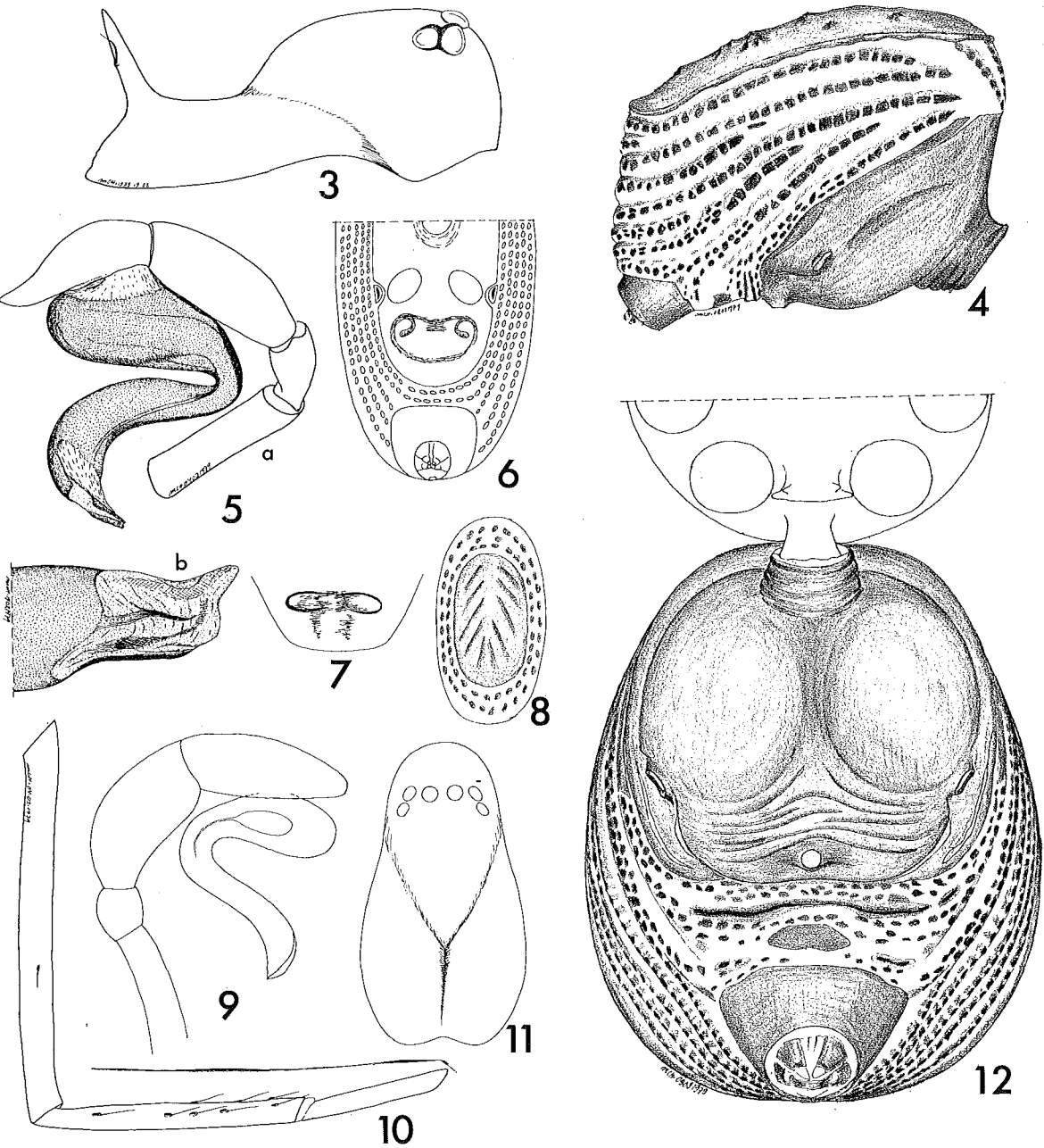
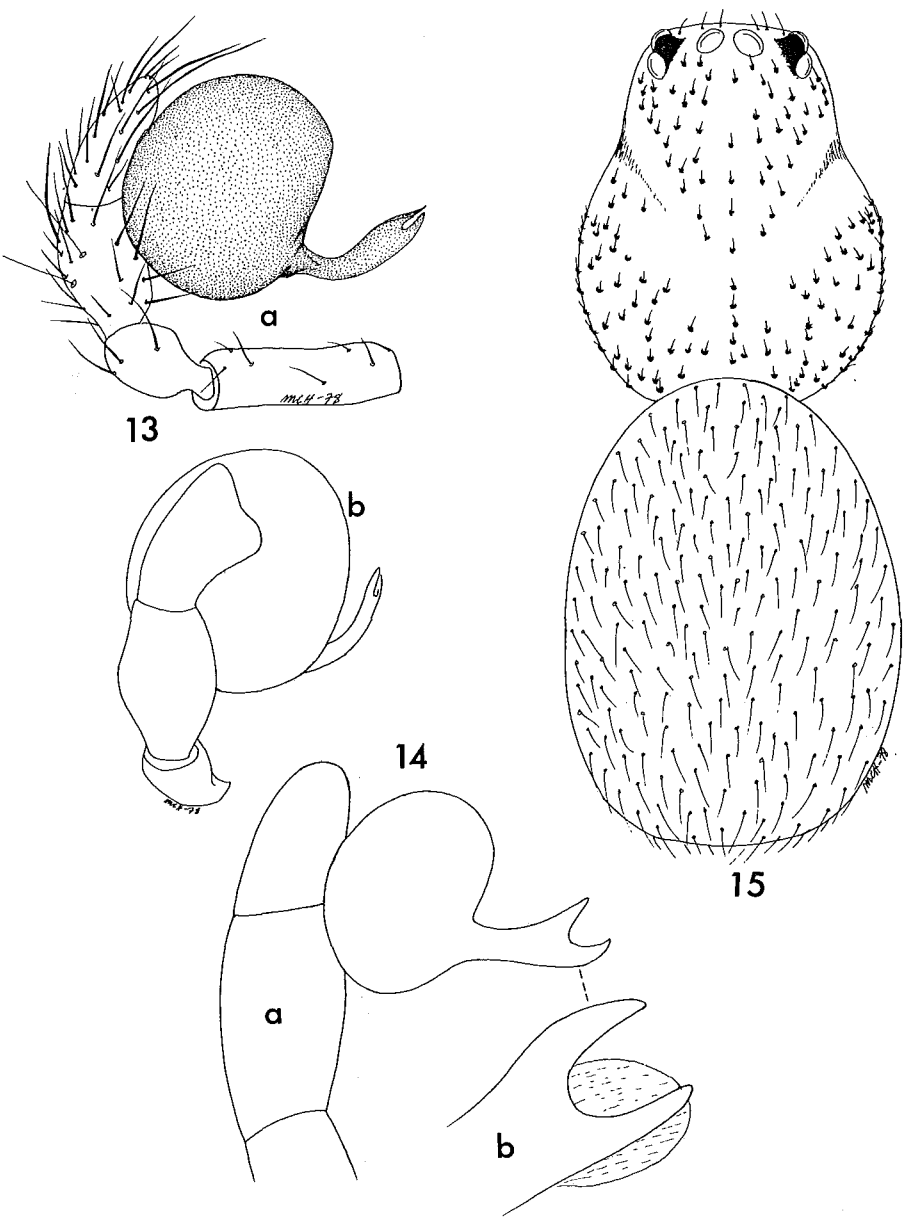


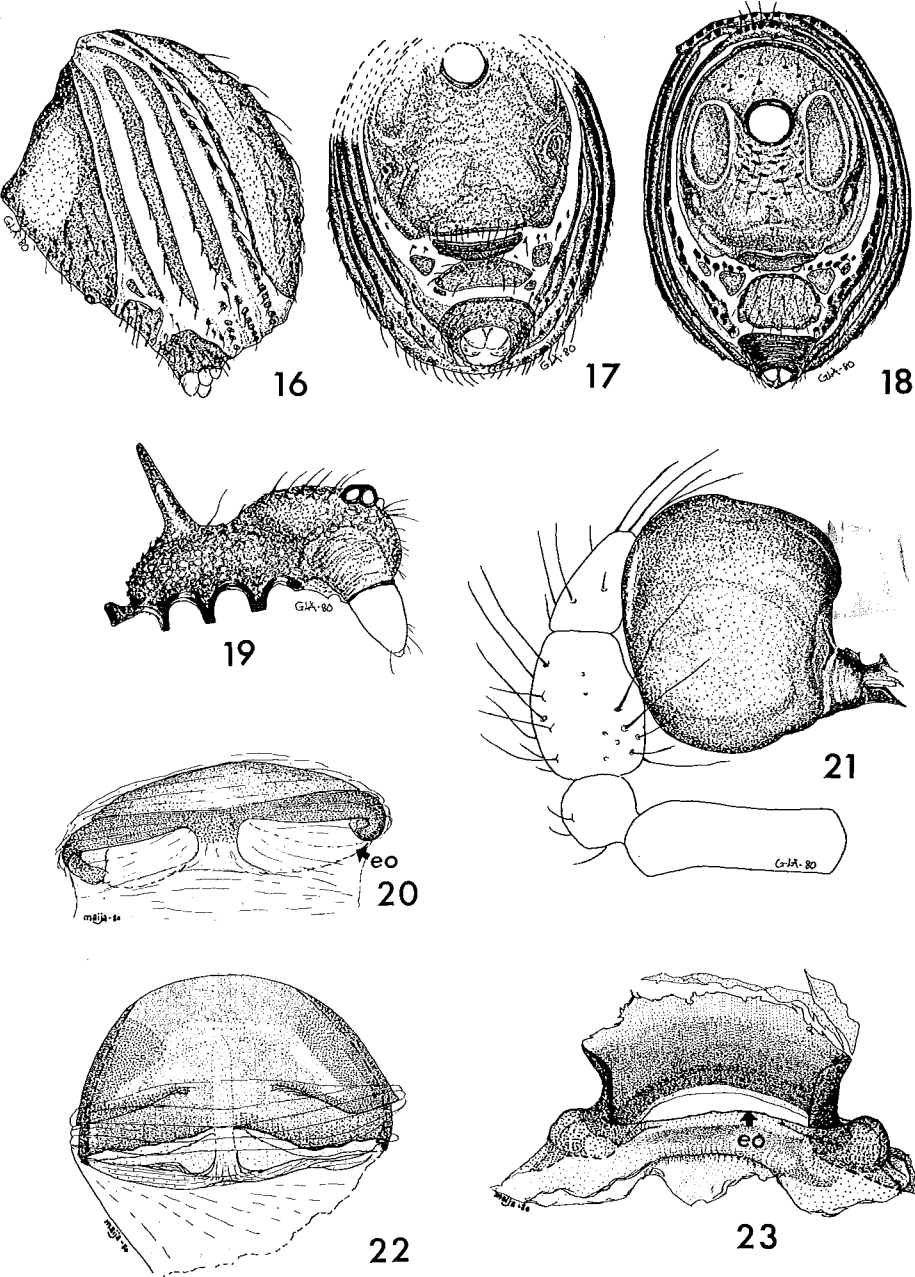
Fig. 2 a—j. Ultrastructure of Tetrablemmidae Tetrablemminae (a—g: *Brignoliella acuminata* (Simon), h—j: *Shearella lilawati* sp. n.). — a: tarsal skin and normal leg hair $\times 5000$. — b: ventral scutum $\times 1000$. — c: hair of dorsal scutum $\times 10\,000$. — d: base of tibial trichobothrium $\times 15\,000$. — e: metatarsal tip with lyriform organs $\times 5000$. — f: base of normal leg hair $\times 3000$. — g: base of normal leg hair $\times 10\,000$. — h: normal leg hairs $\times 10\,000$. — i: modified hair from posterior margin of dorsal scutum $\times 10\,000$. — j: unmodified lateral hair of dorsal scutum $\times 10\,000$.



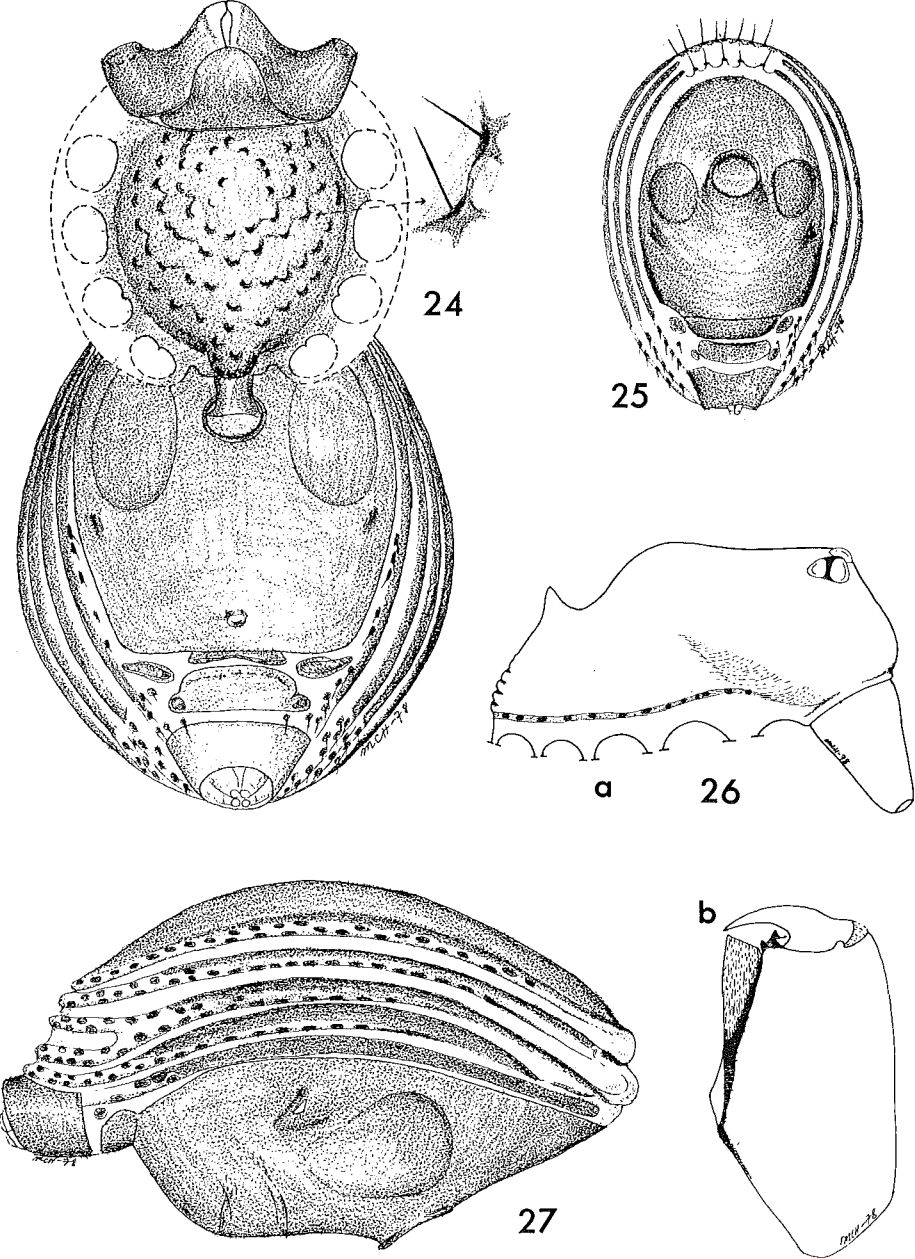
Figs 3—12. *Mirania armata* (Thorell) (3—5, 10, 12), *Perania nigra* (Thorell) (6, 8, 9), and *P. picea* (Thorell) (7, 11). — 3: male carapace laterally (neotype). — 4: male abdomen laterally (neotype). — 5: (a) male palp and (b) apex of embolus (neotype). — 6: abdomen ventrally. — 7: epigynal area. — 8: male abdomen dorsally (lectotype). — 9: male palp (lectotype). — 10: leg I, normal hairs omitted (neotype). — 11: female carapace dorsally (holotype of *P. korinchica*). — 12: male abdomen ventrally (neotype). Figs 6—9 and 11 according to handdrawn sketches.



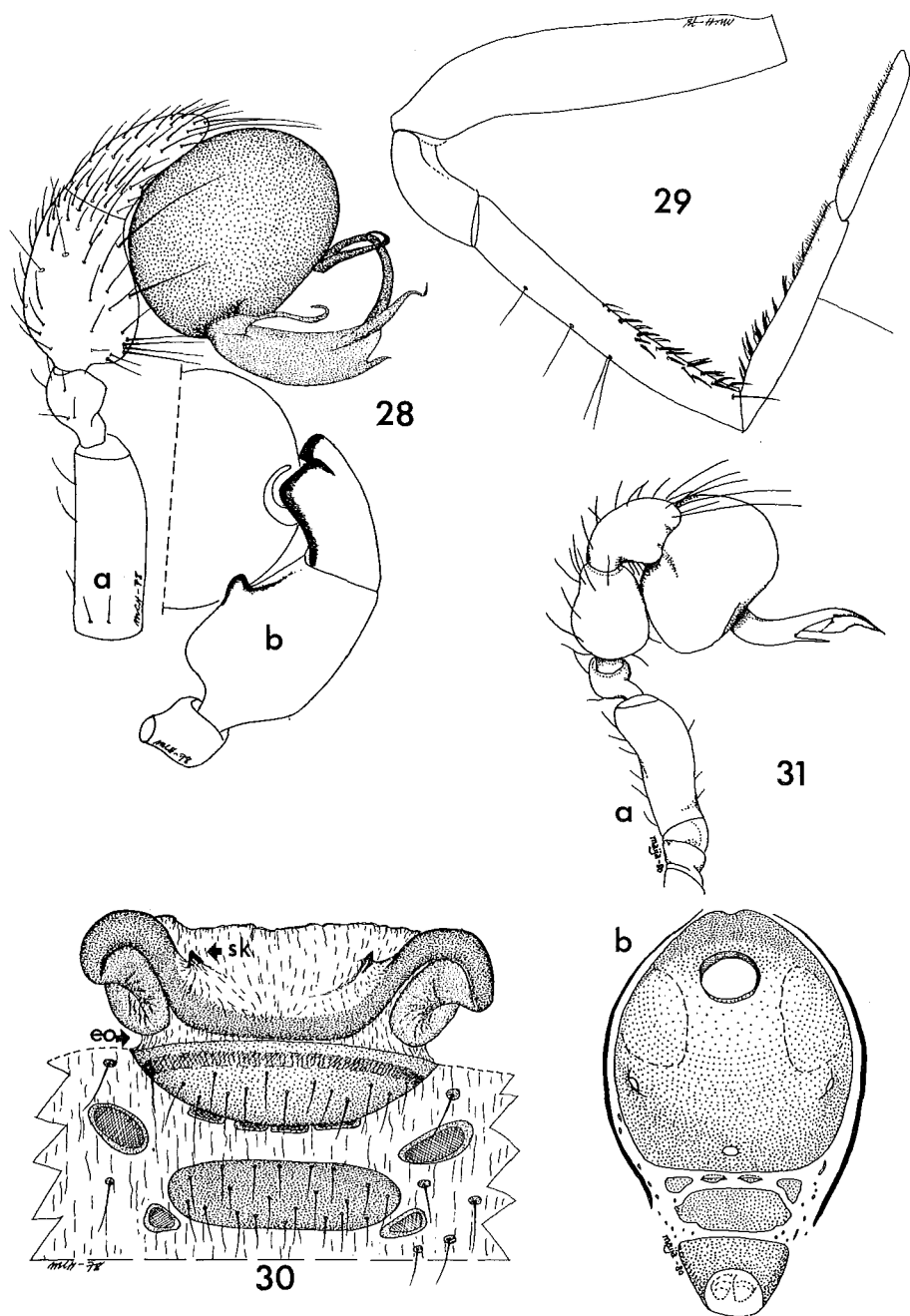
Figs 13—15. *Paculla sulaimani* sp. n. (13, 15) and *P. granulosa* (Thorell) (14). — 13: male palp (a) laterally and (b) dorsally (holotype). — 14: (a) male palp laterally and (b) tip of embolus, both from hand-drawn sketches of holotype. — 15: male carapace and abdomen dorsally (holotype).



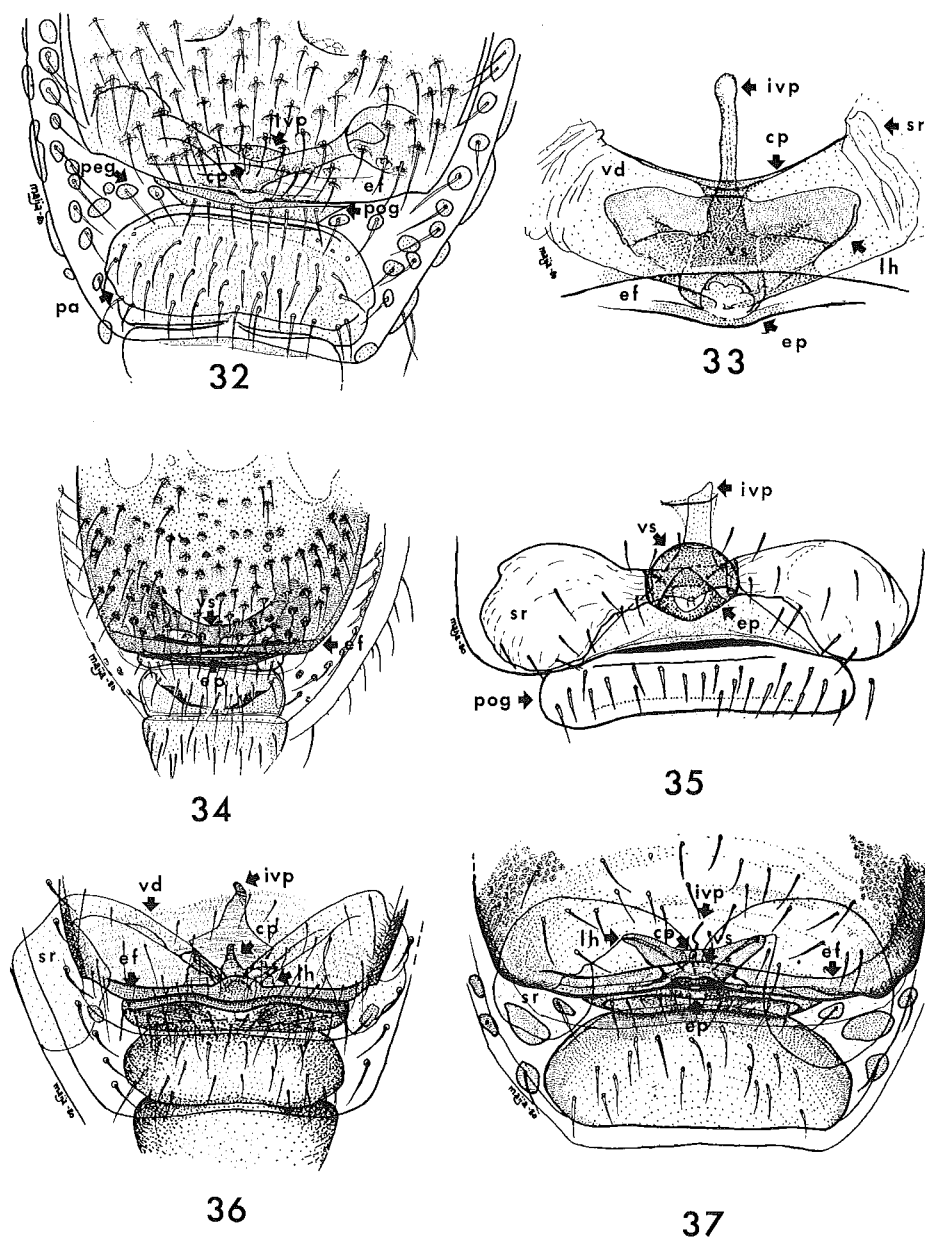
Figs 16—23. *Paculla sulaimani* sp. n. (16), *P. negara* Shear (17, 20, 22), *Lamania bernhardi* (Deeleman-Reinhold) (18, 23), and *L. nirmala* sp. n. (19—21). — 16: male abdomen laterally (holotype). — 17—18: female abdomen ventrally. — 19: female carapace laterally. — 20: sclerotized parts of vulva posteriorly. — 21: male palp (holotype). — 22—23: detached vulval plates ventrally. — eo = epigynal orifice.



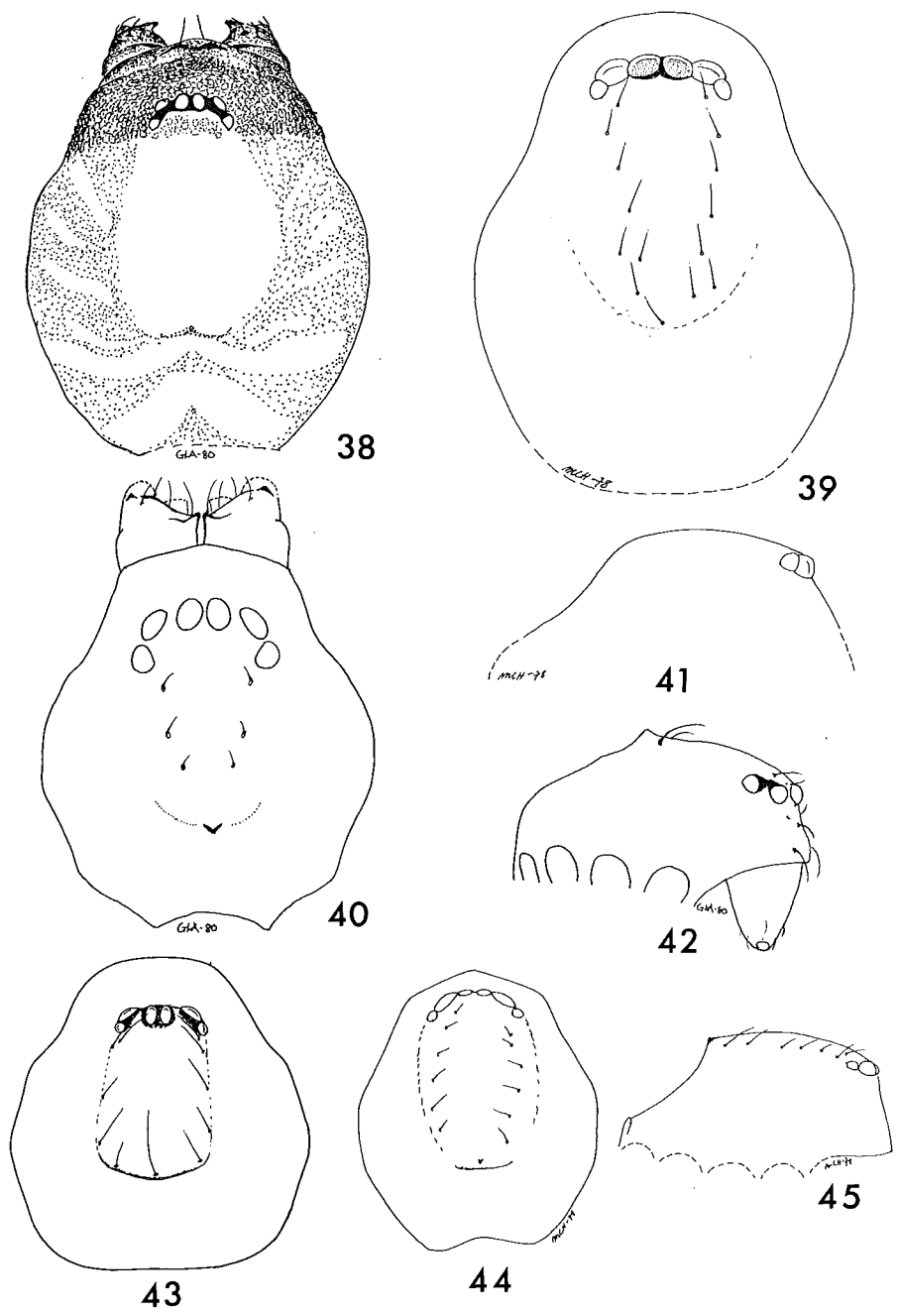
Figs 24—27. *Sabahya kinabaluana* Deeleman-Reinhold. — 24: male ventrally. — 25: female abdomen laterally. — 26: (a) male carapace laterally and (b) male chelicera. — 27 female abdomen ventrally.



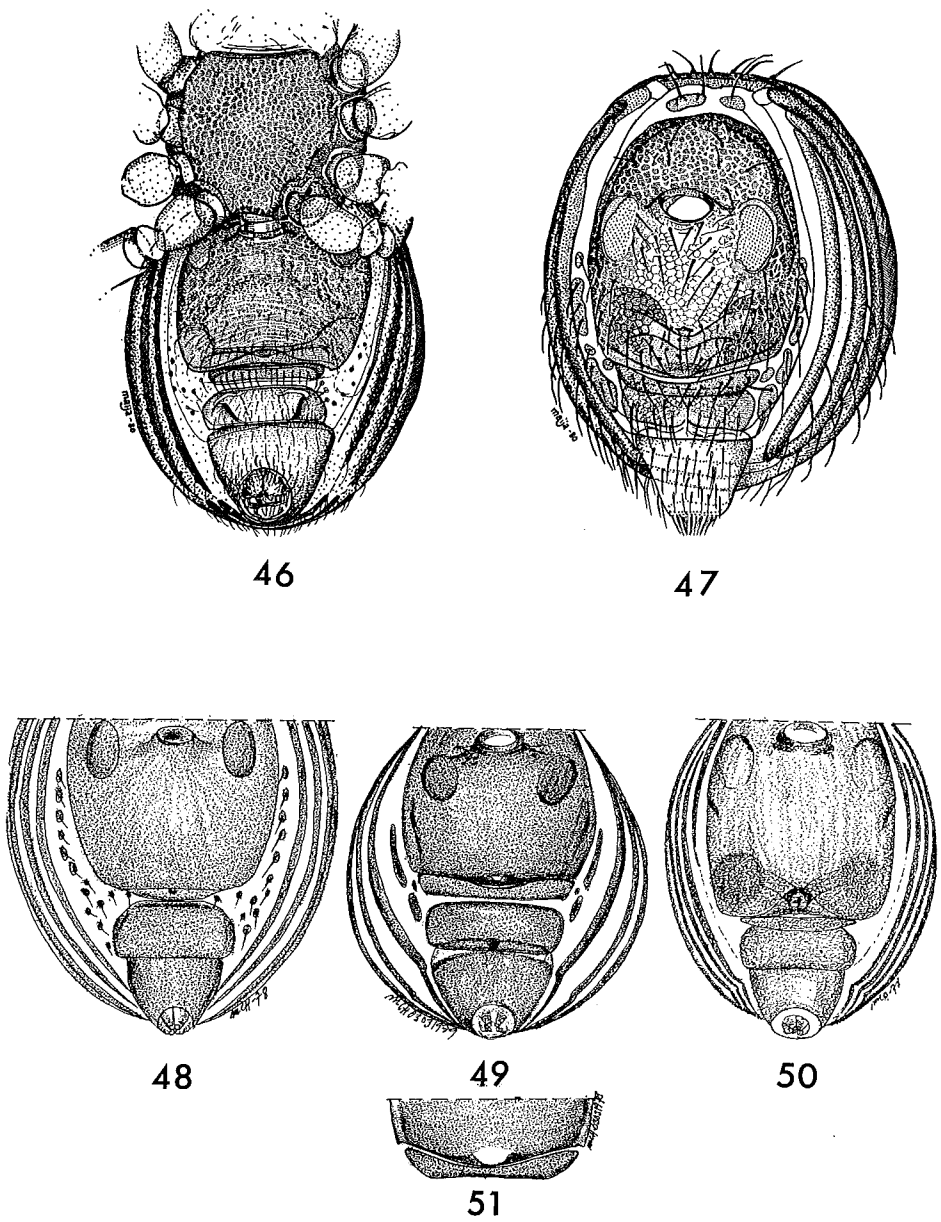
Figs 28—31. *Sabahya kinabaluana* Deeleman-Reinhold (28—30) and "*Paculla*" *cameronensis* Shear (31). — 28: male palp (a) laterally and (b) mesially. — 29: male leg I, normal hairs omitted. — 30: sclerotized parts of vulva with postgenital and preanal plates, pulmonary plate removed. — 31: (a) male palp (holotype) and (b) abdomen ventrally. — eo = epigynal orifice (notch in the margin of pulmonary plate), sk = steering knob for embolus.



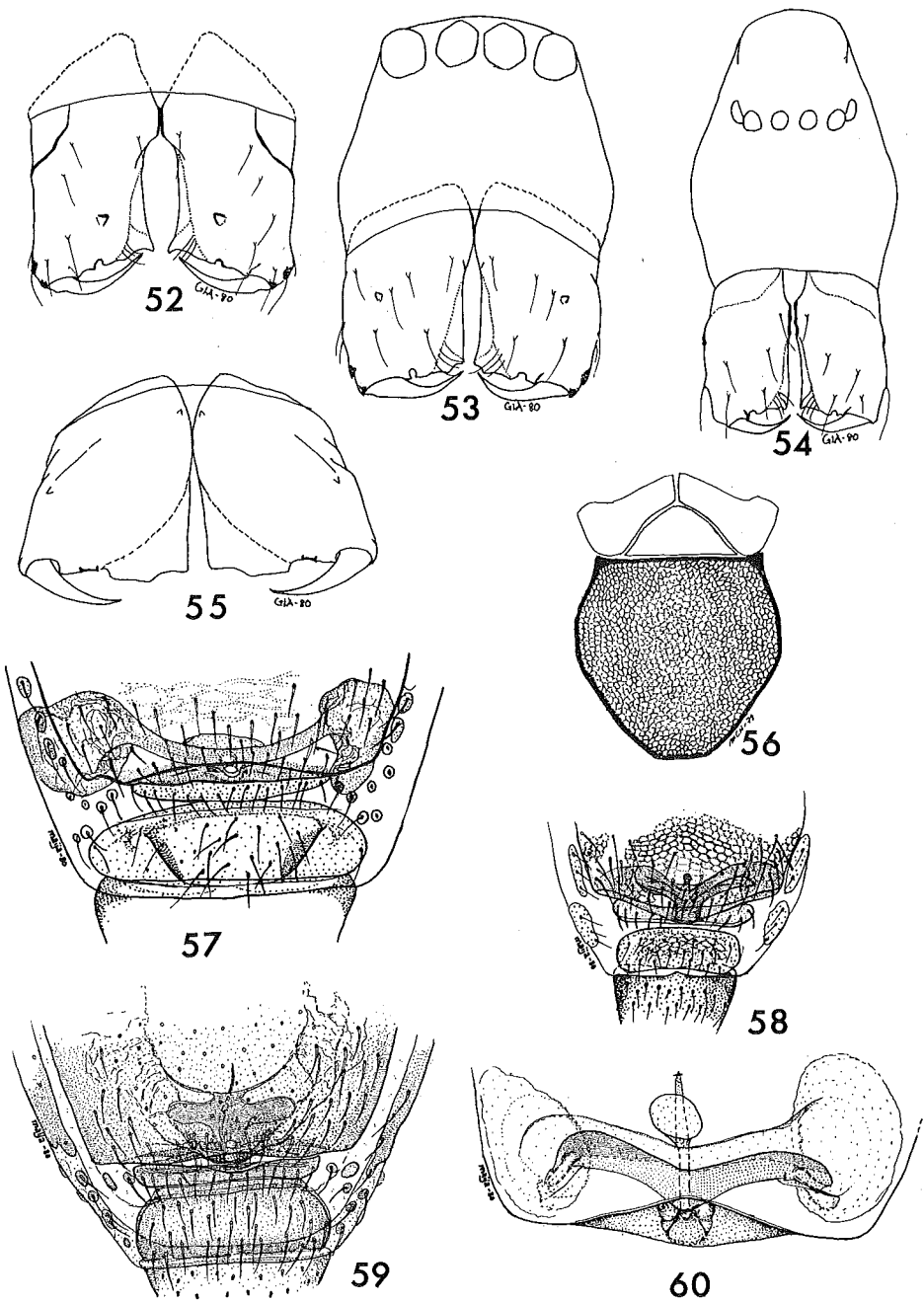
Figs 32—37. Vulval types of different tribes of Tetrablemmine. — 32: *Chavia monticola* sp. n. (Brignoliellini) (holotype). — 33: *Fallablemma greeni* sp. n. (Fallablemmini). — 34: *Brignoliella* (B.) *massai* sp. n. — 35: *Ablemma* (Bannia) *ruohomaekii* sp. n. (Ablemmi). — 36: *Caraimatta blandini* sp. n. (Matini) (holotype). — 37: *Tetrablemma* (T.) *medioculatum gangeticum* ssp. n. (Tetrablemmi). — Abbreviations: ep = epigynal fold, ivp = inner vulval plate, lh = lateral horn, pa = preanal plate, peg = perigenital plates, pog = postgenital plate, sr = seminal receptacula, vd = vulval duct, vs = vulval stem.



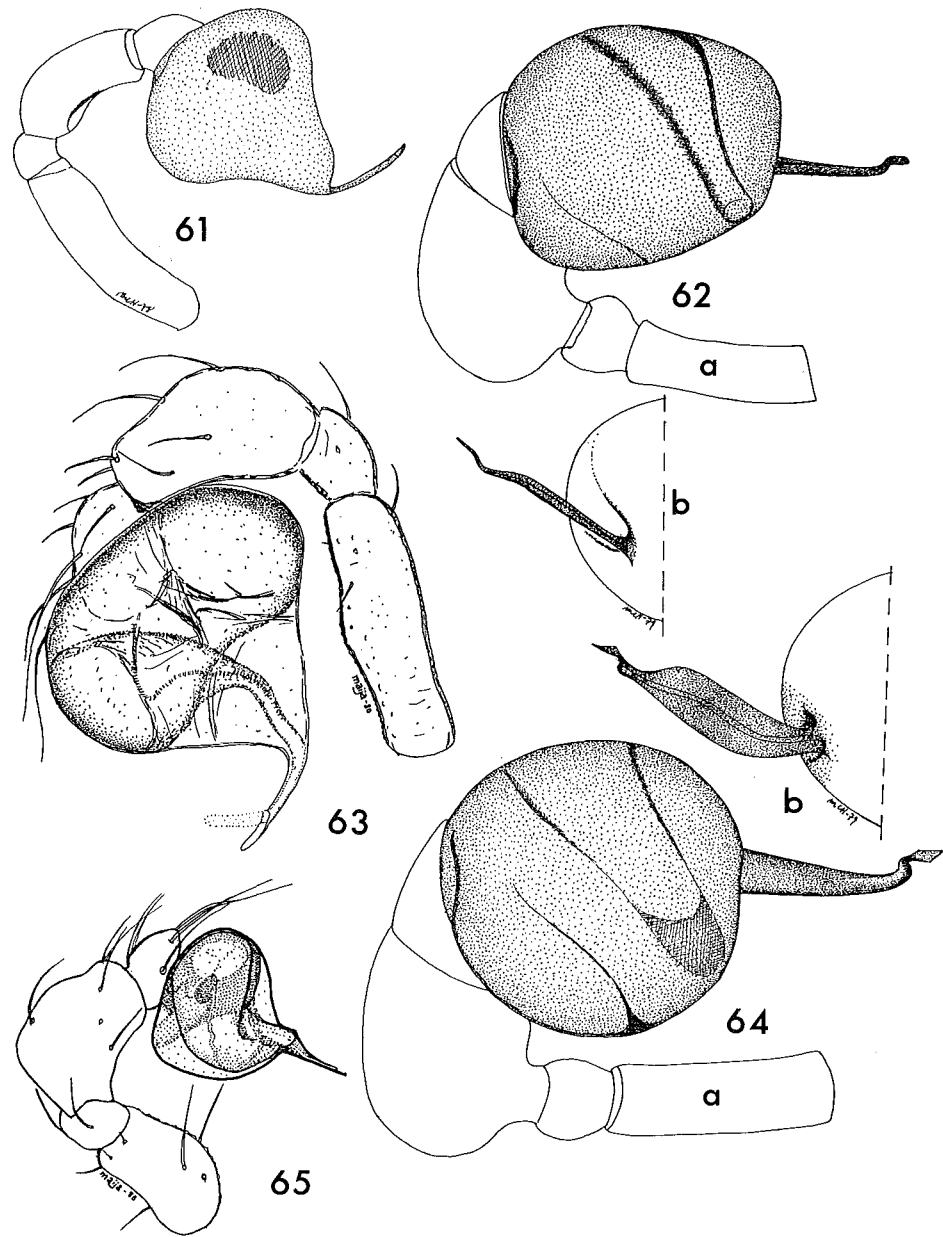
Figs 38—45. *Indicoblemma sheari* Bourne (38), *Chavia monticola* sp. n. (39, 41), *Fallablemma greenei* sp. n. (40, 42), *Singaporemma halongensis* sp. n. (43), and *Afroblemma t. thorelli* (Brignoli) (44—45). — 38: male carapace and chelicerae. — 39: female carapace (holotype). — 40: male carapace and chelicerae. — 41: female carapace (holotype). — 42: female carapace and chelicerae. — 43—44: male carapace dorsally. — 45: male carapace laterally.



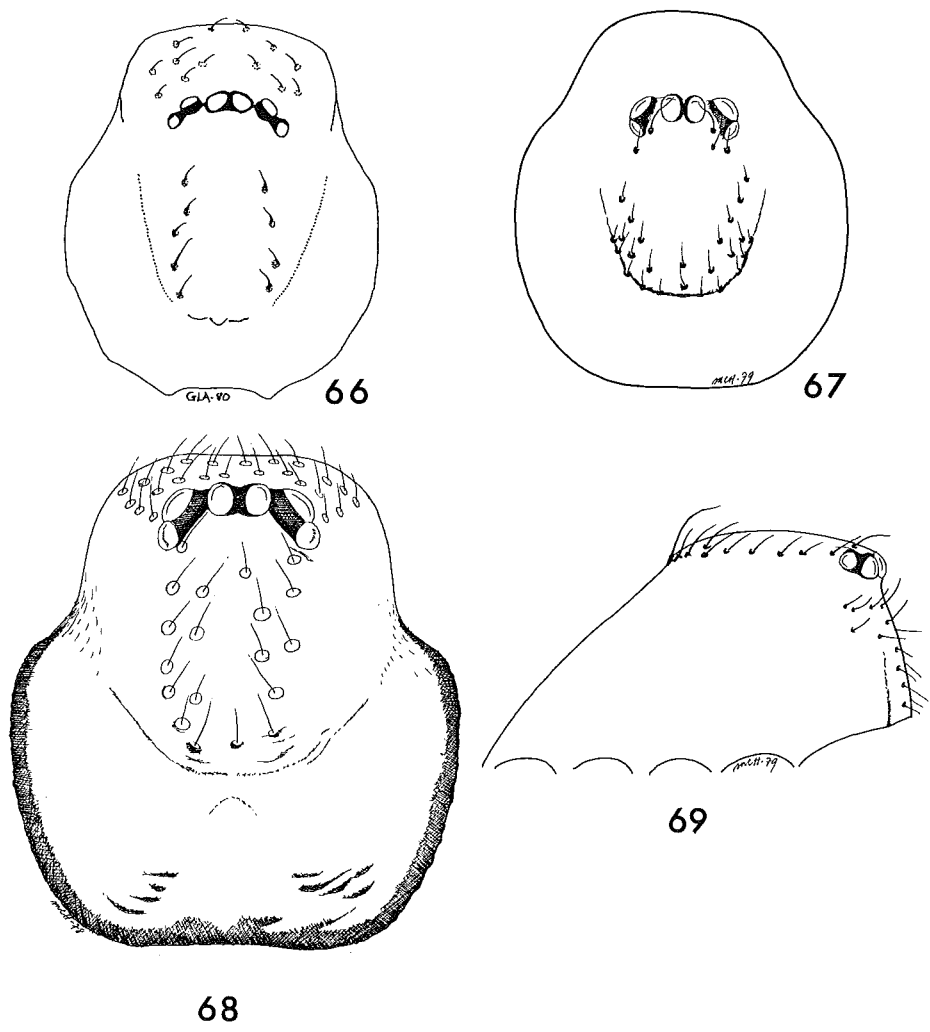
Figs 46—51. *Indicoblemma sheari* Bourne (46), *Singaporemma adjacens* sp. n. (27, 51), *Chavia monticola* sp. n. (48), *Singaporemma halongensis* sp. n. (49), and *Afroblemma t. thorelli* (Brignoli) (50). — 46: female carapace and abdomen ventrally. 47—50: female abdomen ventrally. — 51: epigynal area.



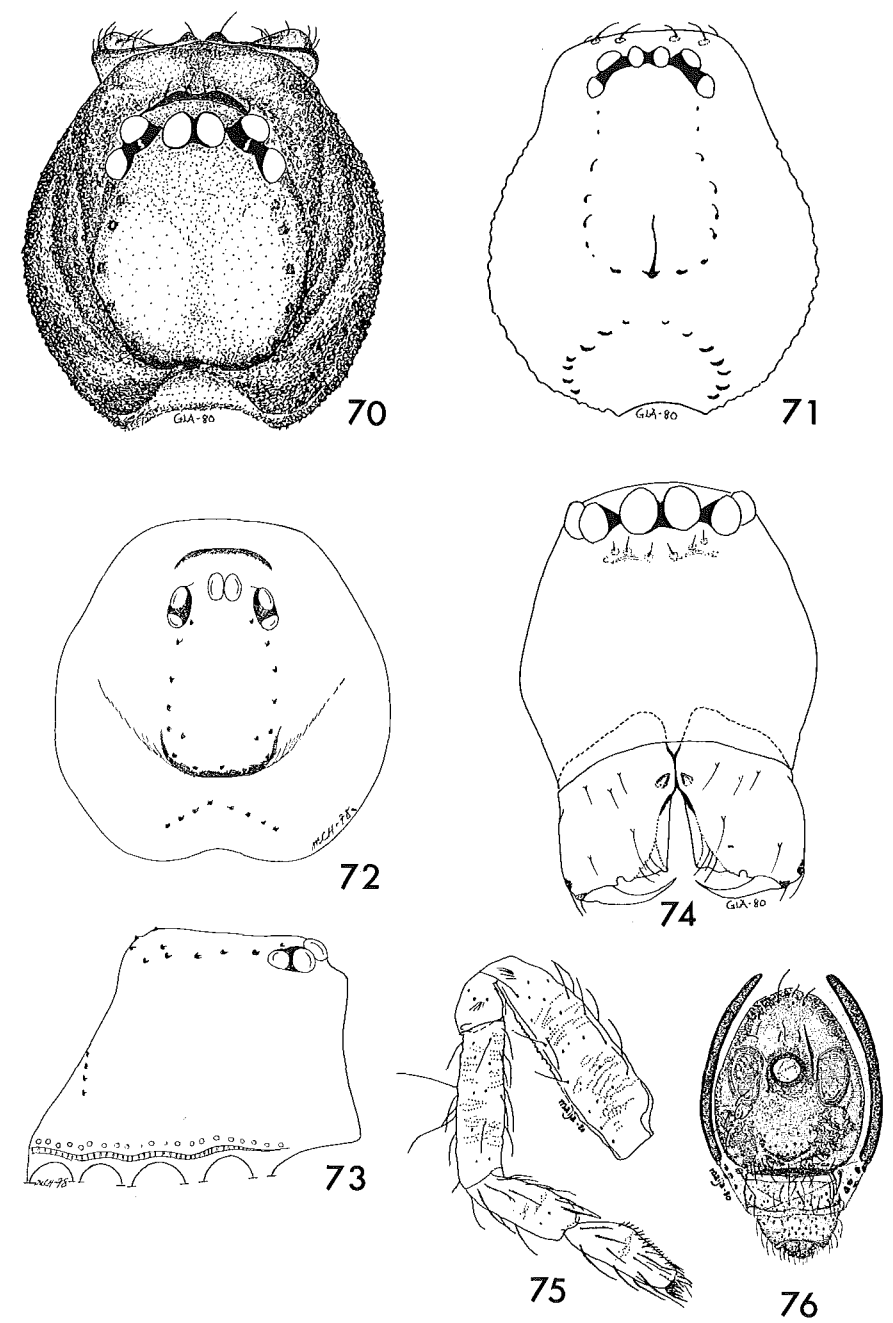
Figs 52—60. *Indicoblemma sheari* Bourne (52, 57), *Fallablemma greeni* sp. n. (53, 59), *Singaporemma halongensis* sp. n. (54, 58), *Afroblemma t. thorelli* (Brignoli) (55, 60), and *Chavia monticola* sp. n. (56). — 52: male chelicerae. — 53: male clypeus and chelicerae. — 54: male clypeus and chelicerae. — 55: male chelicerae. — 56: sternum, gnathocoxae, and labium (holotype). — 57—59: female epigynal area and cleared vulva. — 60: cleared vulva.



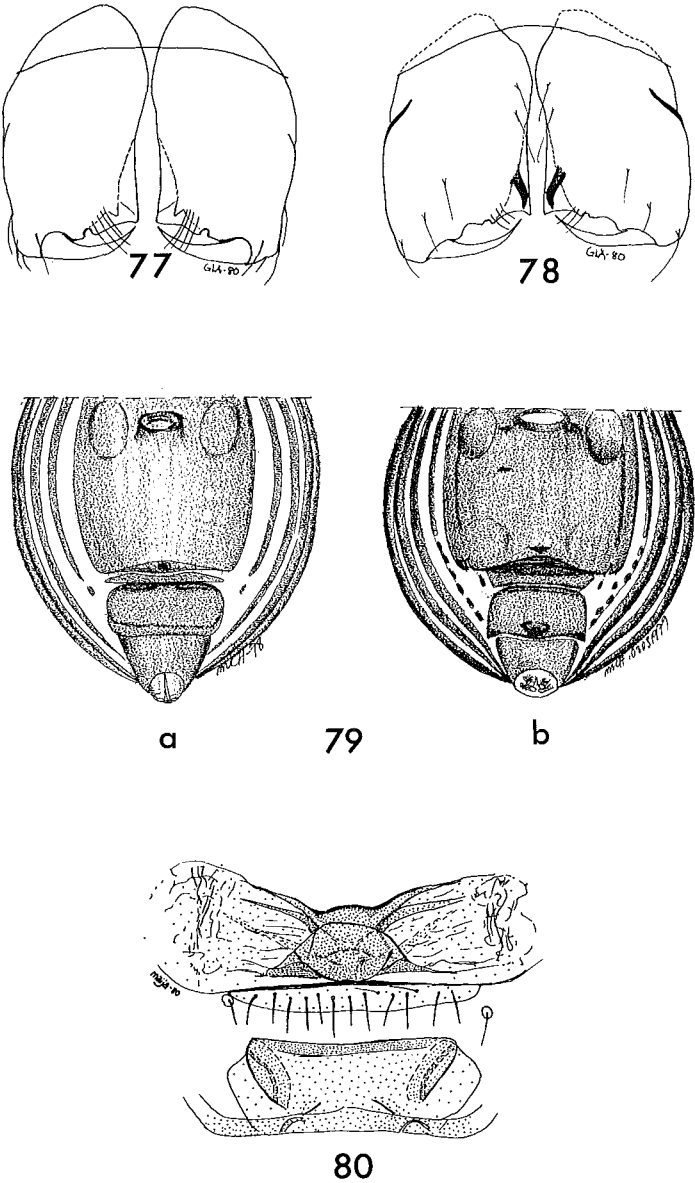
Figs 61—65.. *Afroblemma t. thorelli* (Brignoli) (61), *Singaporemma halongensis* sp. n. (62), *Fallablemma greeni* sp. n. (63), *Singaporemma adjacens* sp. n. (64), and *Indicoblemma sheari* Bourne (65). — 61, 63, 65: male palp laterally. — 62, 64: (a) male palp laterally, and b) embolus mesially.



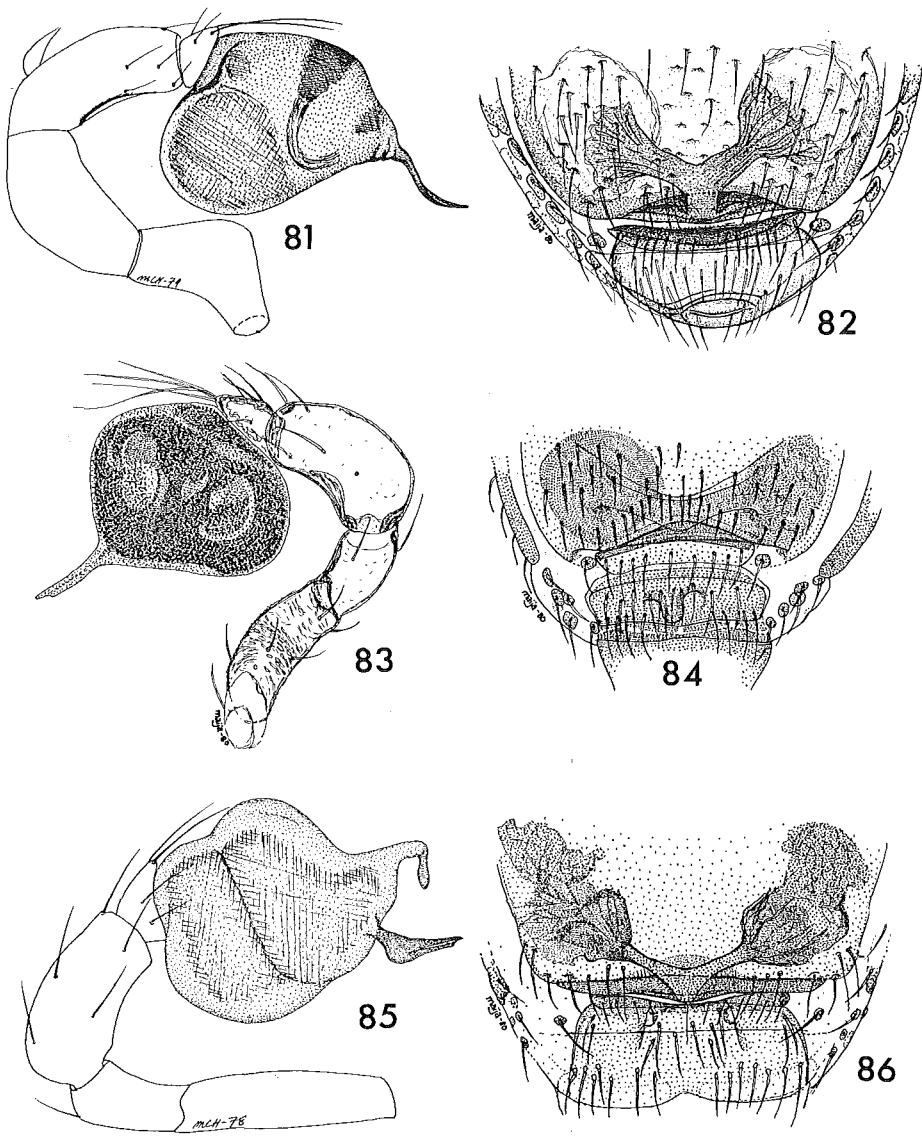
Figs 66—69. *Pahanga centenialis* sp. n. (66), *P. lilisari* sp. n. (67, 69), and *P. diyaluma* sp. n. (68). — 66, 68: female carapace dorsally. — 67: male carapace dorsally. — 69: female carapace laterally.



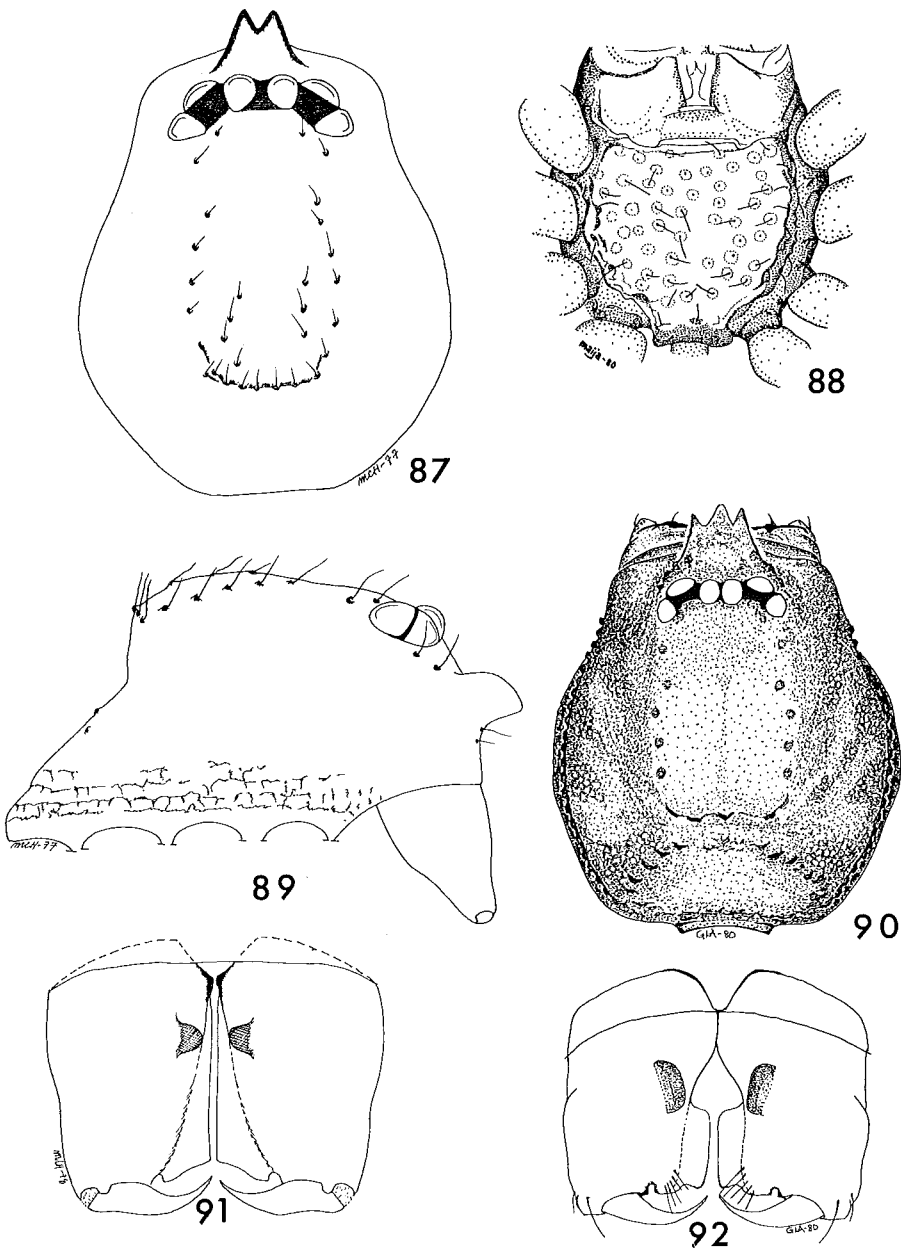
Figs 70—76. *Borneomma (Oleoblemma) yuata* sp. n. (70, 71, 74—75), *B. (B.) roberti* Deeleman-Reinhold (72, 73, 75), and *Pahanga centenialis* sp. n. (76). — 70: male carapace and chelicerae dorsally. — 71: female carapace. — 72: male carapace dorsally. — 73: male carapace laterally. — 74: male clypeus and chelicerae. — 75: male leg I. — 76: female abdomen ventrally.



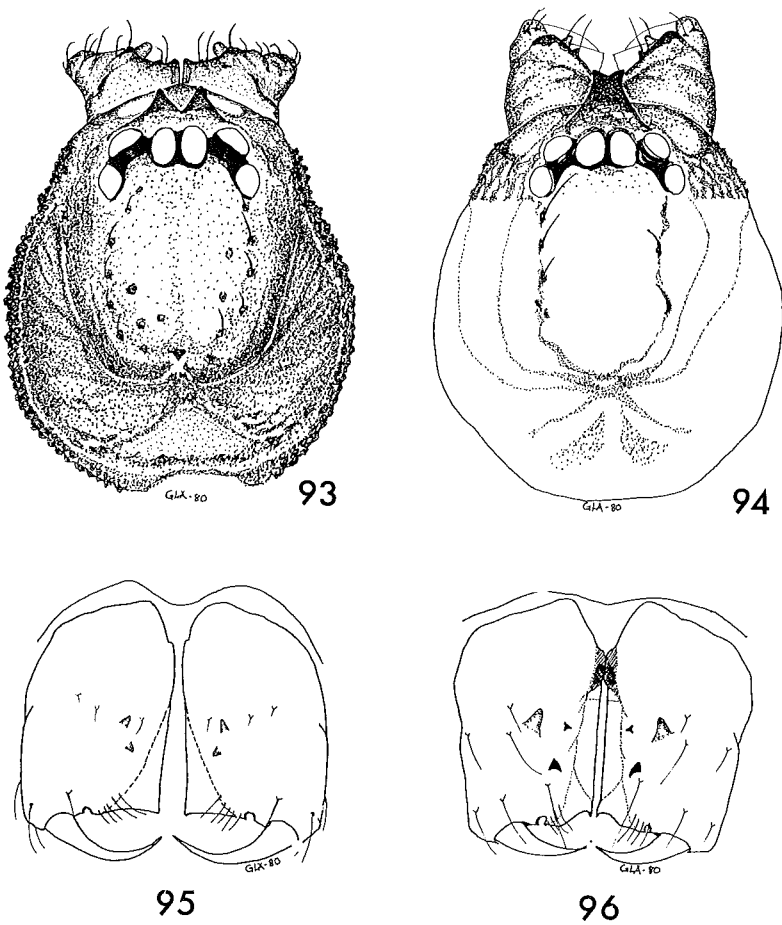
Figs 77—80. *Pahanga centenialis* sp. n. (77), *P. lilisari* sp. n. (78, 79b), *P. diyaluma* sp. n. (79a), and "*Brignoliella*" *sarawak* Shear (80). — 77: female chelicerae. — 78: male chelicerae. — 79a, b: female abdomen ventrally. — 80: female epigynal area and cleared vulva.



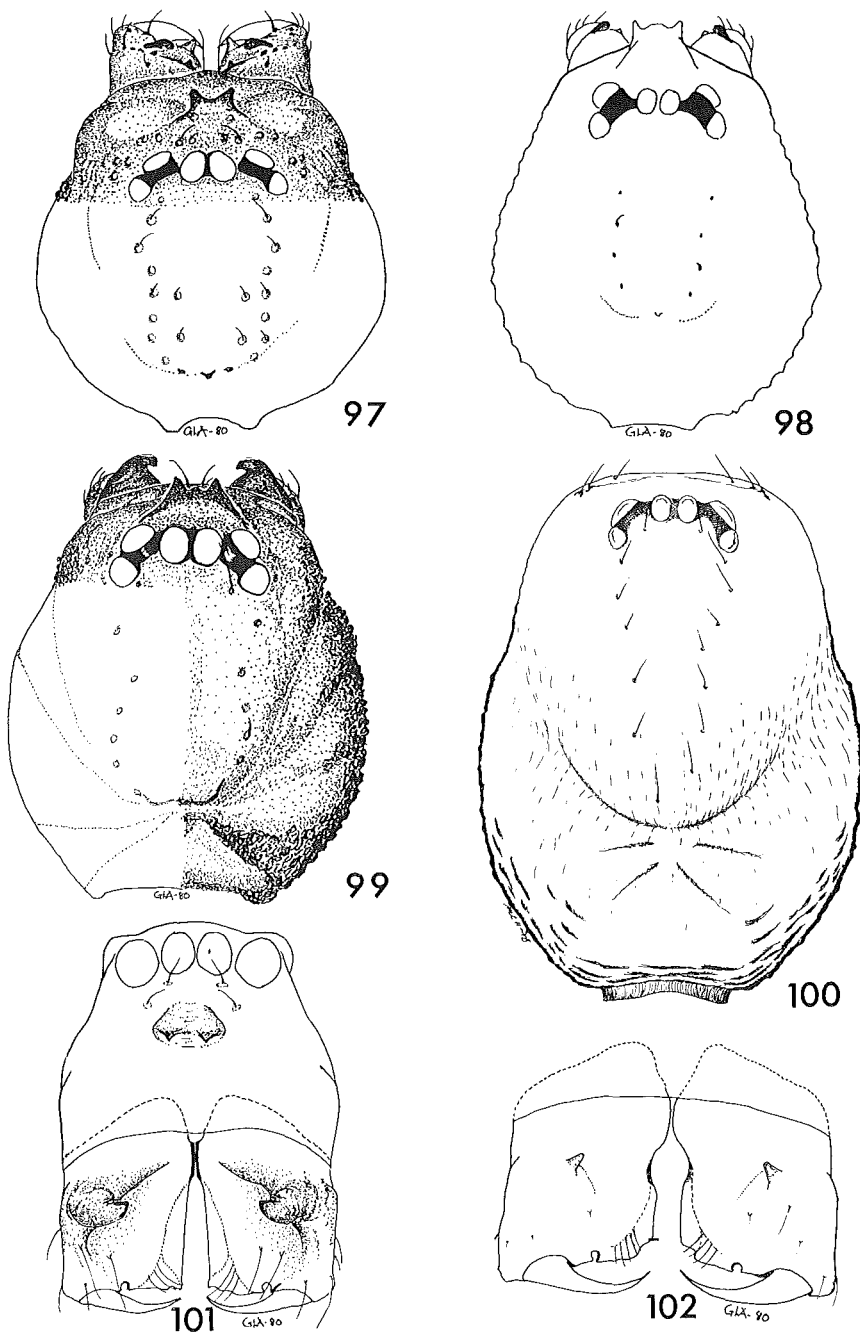
Figs 81—86. *Pahanga lilisari* sp. n. (81, 82), *Borneomma* (*Oleoblemma*) *yuata* sp. n. (83, 84), *B. (B.) roberti* Deeleman-Reinhold (85), and *Pahanga centenialis* sp. n. (86). — 81, 83, 85: male palp laterally. — 82, 84, 86: epigynal area and cleared vulva.



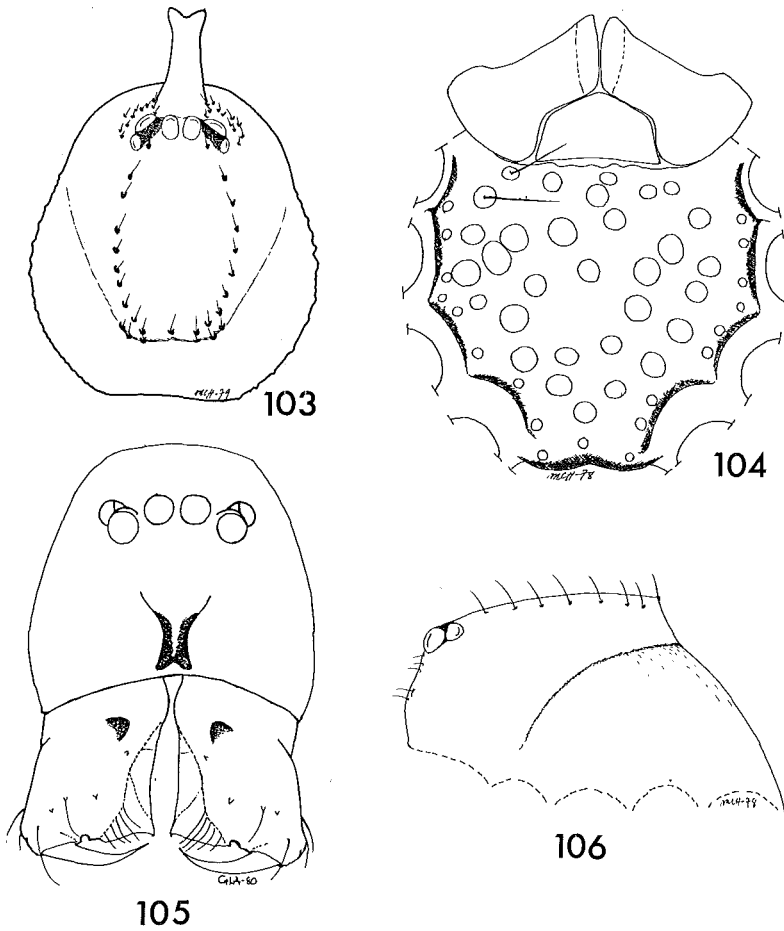
Figs 87—92. *Brignoliella (B.) acuminata* (Simon) (87—89, 91) and *B. (B.) trifida* sp. n. (90, 92). — 87: male carapace. — 88: female sternum. — 89: male carapace laterally. — 90: male carapace dorsally. — 91—92: male chelicerae.



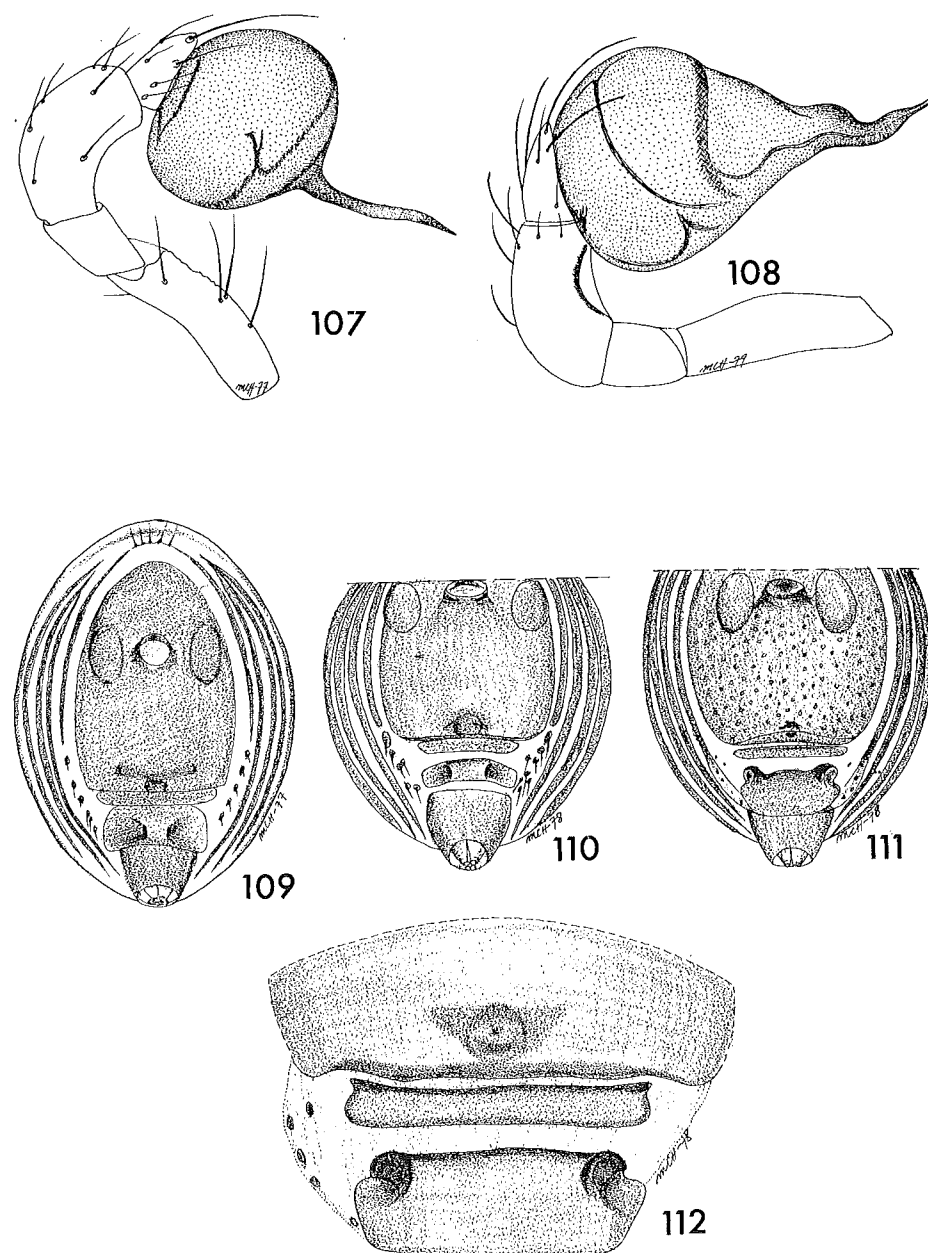
Figs. 93—96. *Brignoliella (B.) massai* sp. n. (93, 95) and *B. (B.) vulgaris* sp. n. (94, 96). — 93—94: male chelicerae.



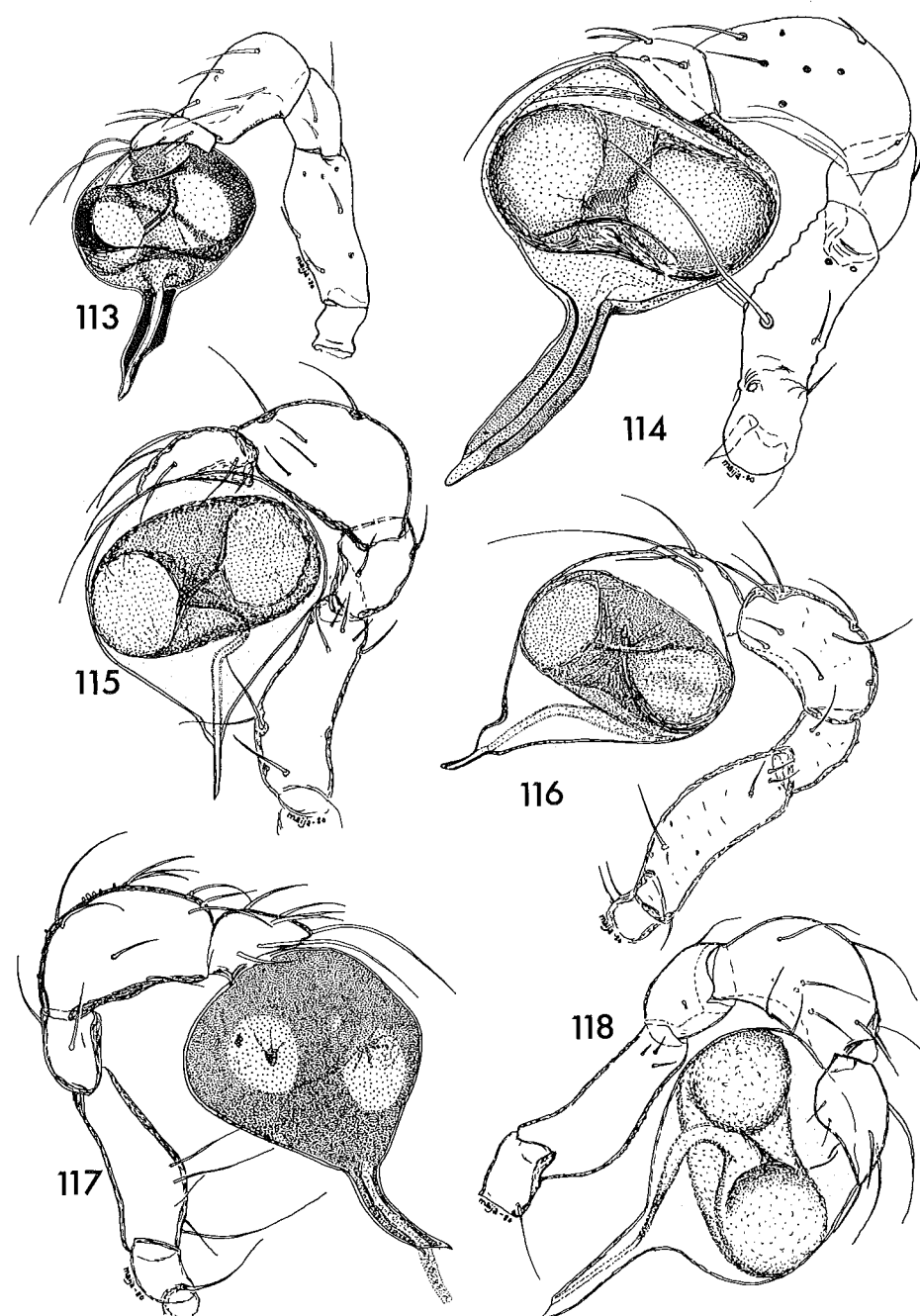
Figs 97—102. *Brignoliella* (*B.*) *maros* sp. n. (97), *B.* (*B.*) *martensi* (Brignoli) (98, 100, 102) and *B.* (*B.*) *carmen* sp. n. (99, 101). — 97: male carapace and chelicerae anterodorsally to show clypeal surface (holotype). — 98—99: male carapace and chelicerae dorsally. — 100: female carapace dorsally (holotype). — 101: male clypeus and chelicerae. — 102: male chelicerae.



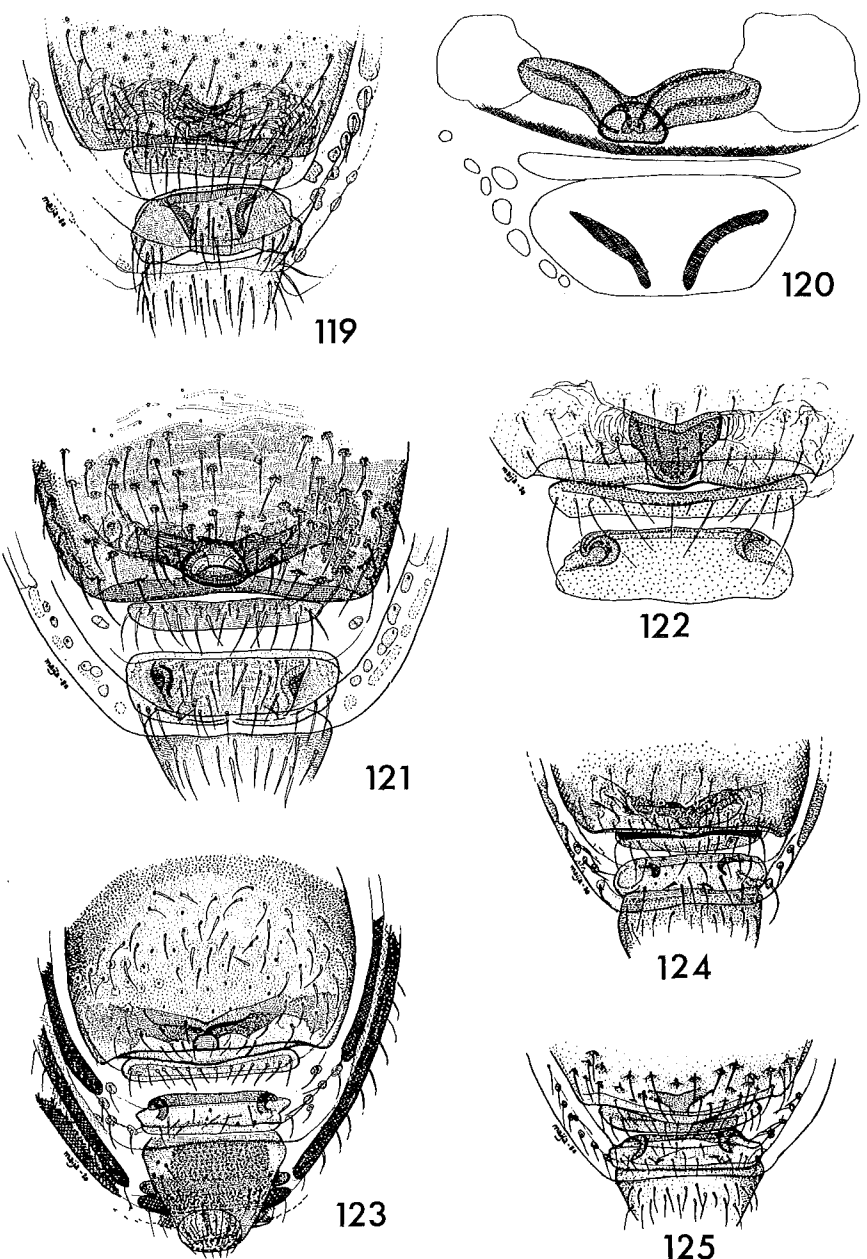
Figs 103—106. *Brignoliella* (*Ceratoblemma*) *michaeli* sp. n. — 103: male carapace (holotype). — 104: female sternum. — 105: male clypeus and chelicerae (holotype). — 106: female carapace laterally.



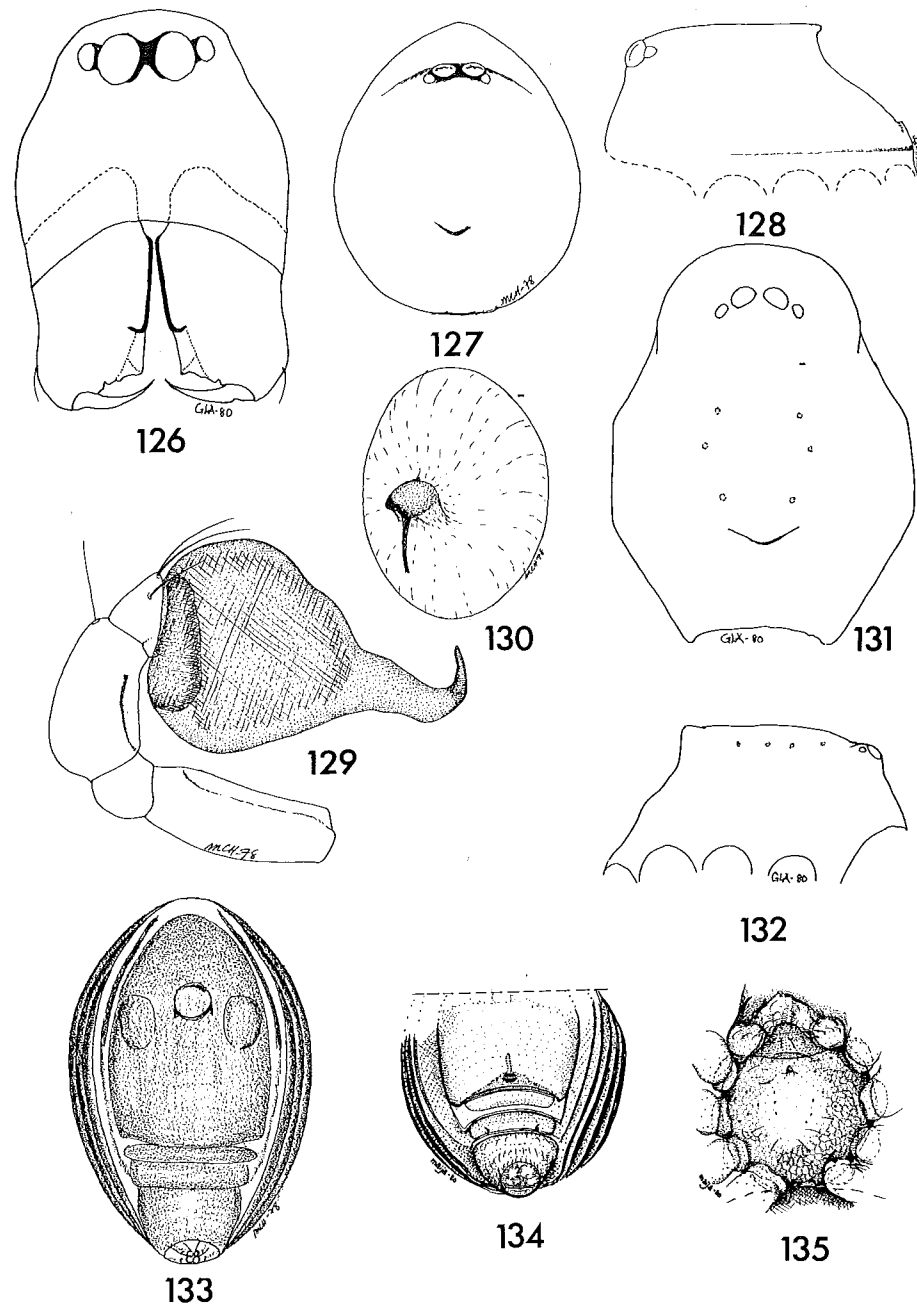
Figs 107—112. *Brignoliella (B.) acuminata* (Simon) (107, 109), *B. (Ceratoblemma) michaeli* sp. n. (108, 111), *B. (B.) vitiensis* sp. n. (110), and *B. (B.) martensi* (Brignoli) 112). — 107—108: male palp. — 109—111: female abdomen ventrally. — 112: epigynal area (holotype).



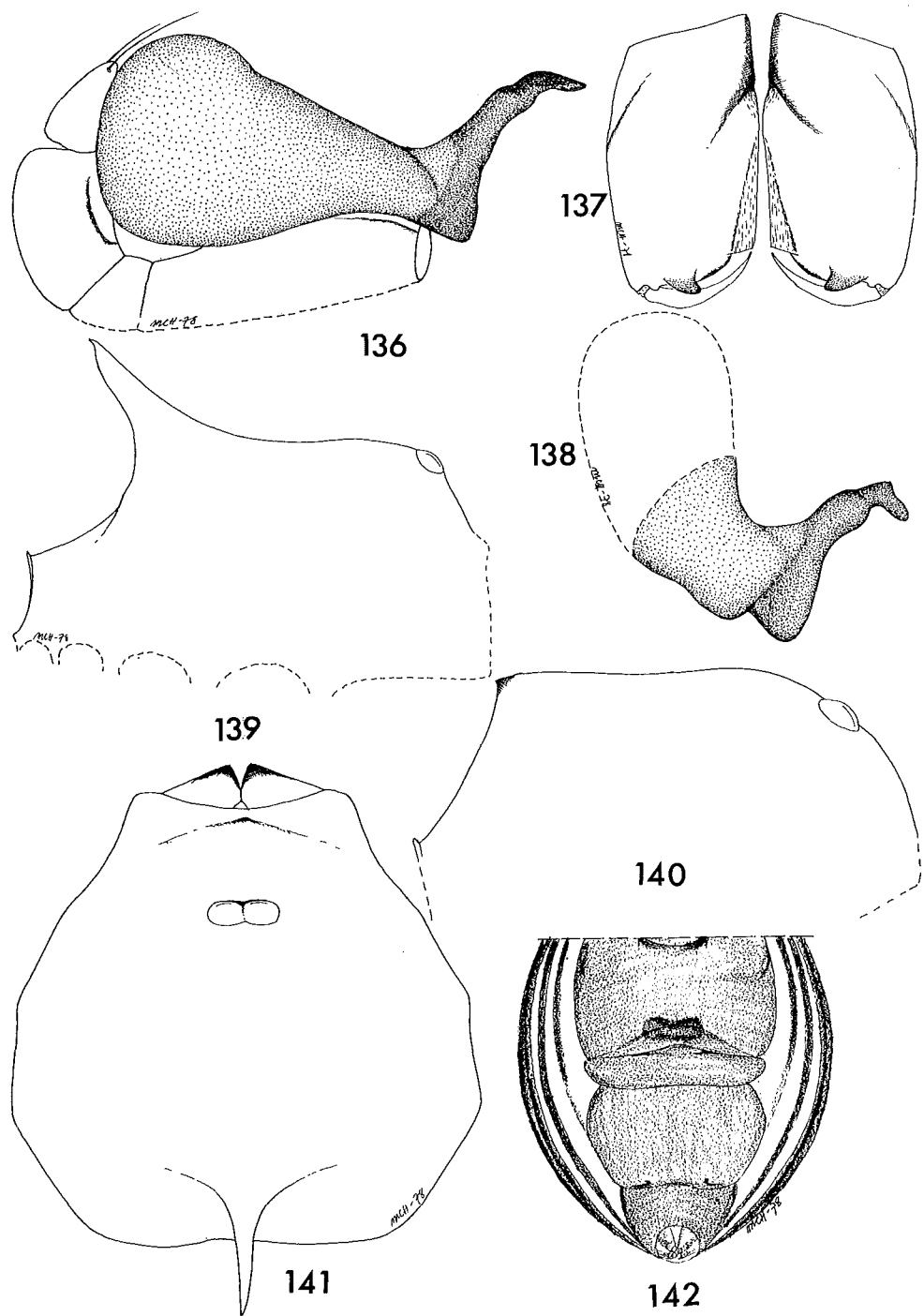
Figs 113—118. *Brignoliella (B.) carmen* sp. n. (113), *B. (B.) trifida* sp. n. (holotype) (114). — *B. (B.) massai* sp. n. (115), *B. (B.) maros* sp. n. (holotype) (116), *B. (B.) martensi* (Brignoli) (117), and *B. (B.) vulgaris* sp. n. (118). — 113—118: male palp.



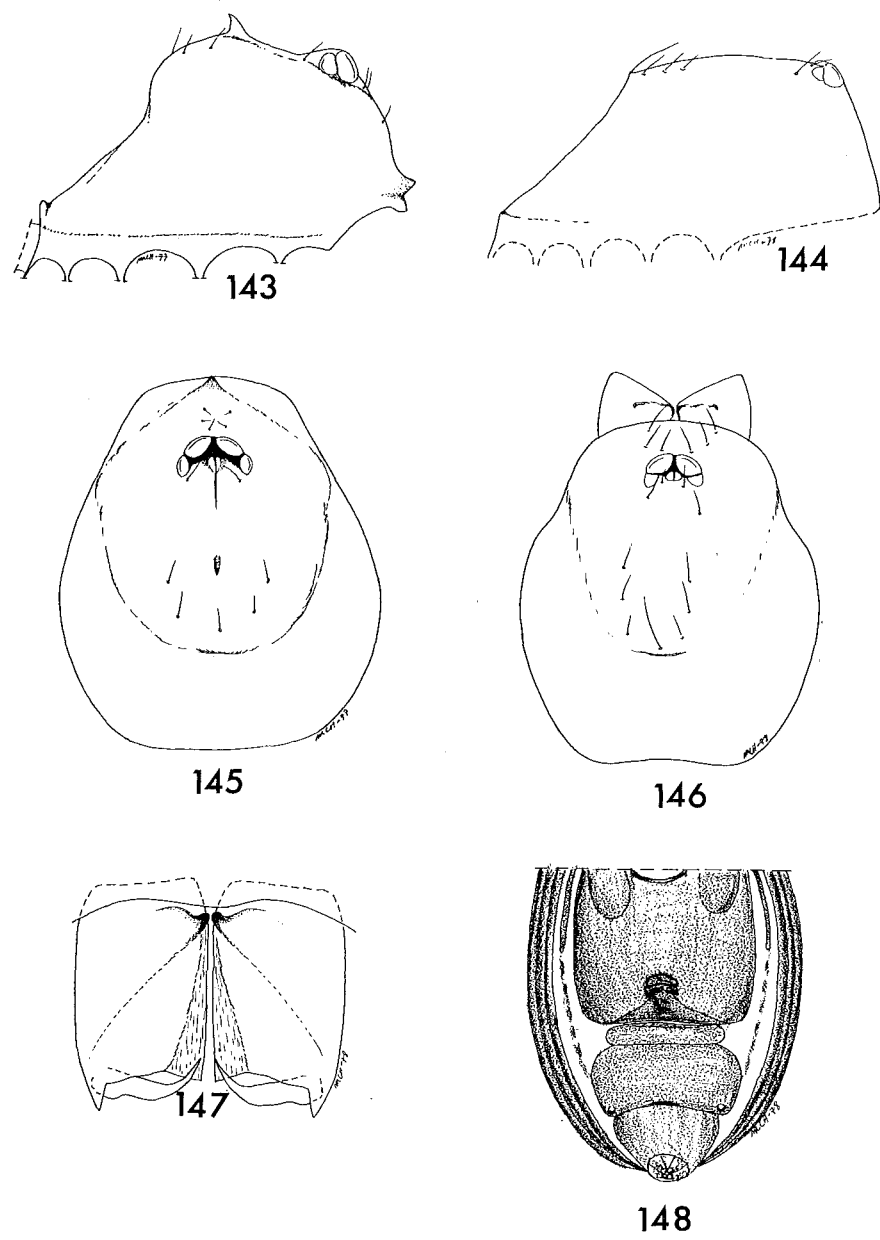
Figs 119—125. *Brignoliella* (*B.*) *bicornis* (Simon) (119), *B. (B.) acuminata* (Simon) (120), *B. (B.) carmen* sp. n. (121), *B. (B.) vulgaris* sp. n. (122), *B. (B.) klabati* sp. n. (holotype) (123), *B. (B.) massai* sp. n. (124), and *B. (B.) maros* sp. n. (125). — 119—125: female epigynal area with cleared vulva and preanal plate.



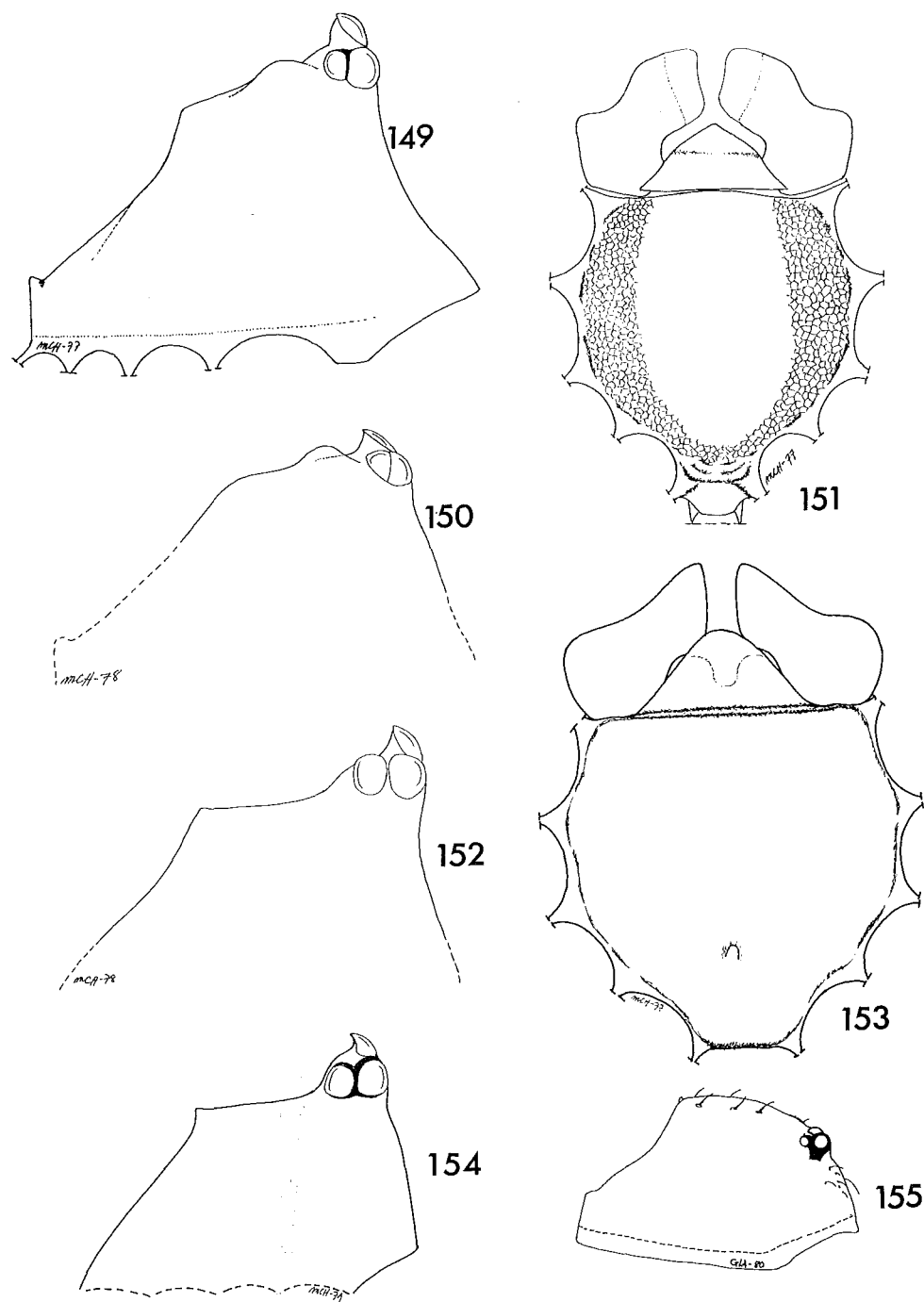
Figs 126—135. *Sulaimania vigelandi* sp. n. (126—130, 133) and *Ablemma (A.) sternofoveata* sp. n. (131—132, 134—135). — 126: male clypeus and chelicerae. — 127: male carapace dorsally. — 128: male carapace laterally. — 129: male palp. — 130: male bulbus ventrally. — 131: female carapace dorsally. — 132: female carapace laterally. — 133: male abdomen ventrally. — 134: female abdomen ventrally. — 135: female sternum.



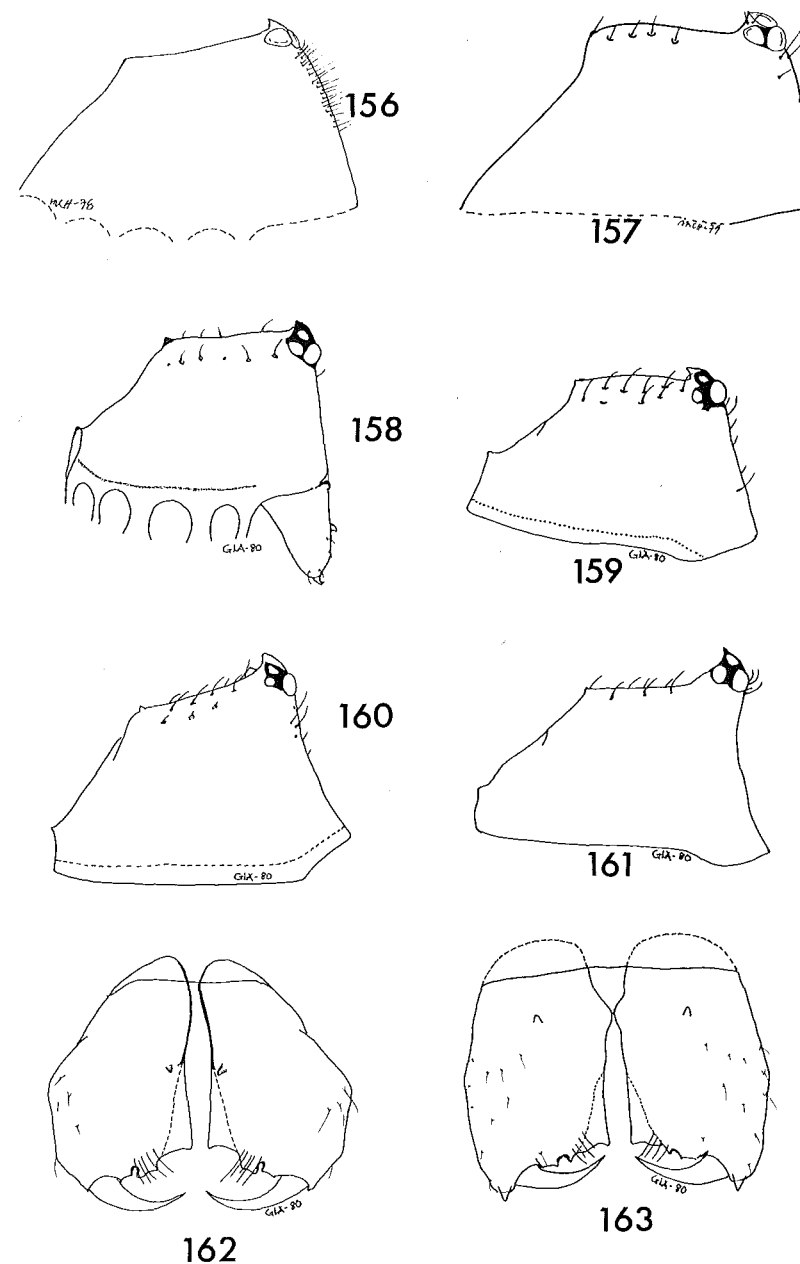
Figs 136—142. *Ablemma (A.) baso* Roewer (type material). — 136: male palp. — 137: male chelicerae. — 138: male bulbus anterolaterally. — 139: male carapace laterally. — 140: female carapace laterally. — 141: male carapace dorsally. — 142: female abdomen ventrally.



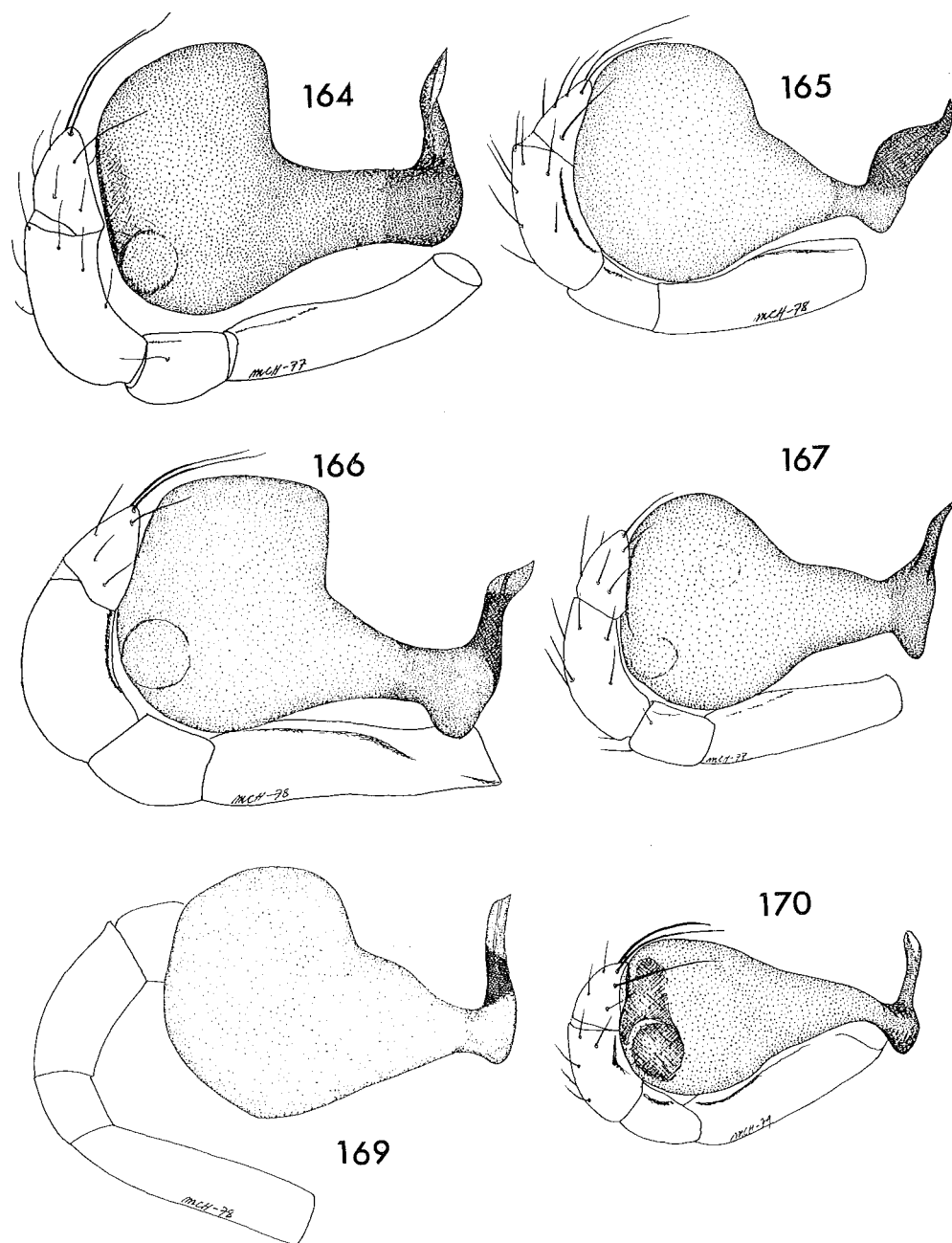
igs 143—148. *Ablemma (Bannia) ruohomaekii* sp. n. — 143: male carapace laterally. — 144: female carapace laterally. — 145: male carapace dorsally. — 146: female carapace dorsally. — 147: male chelicerae. — 148: female abdomen ventrally.



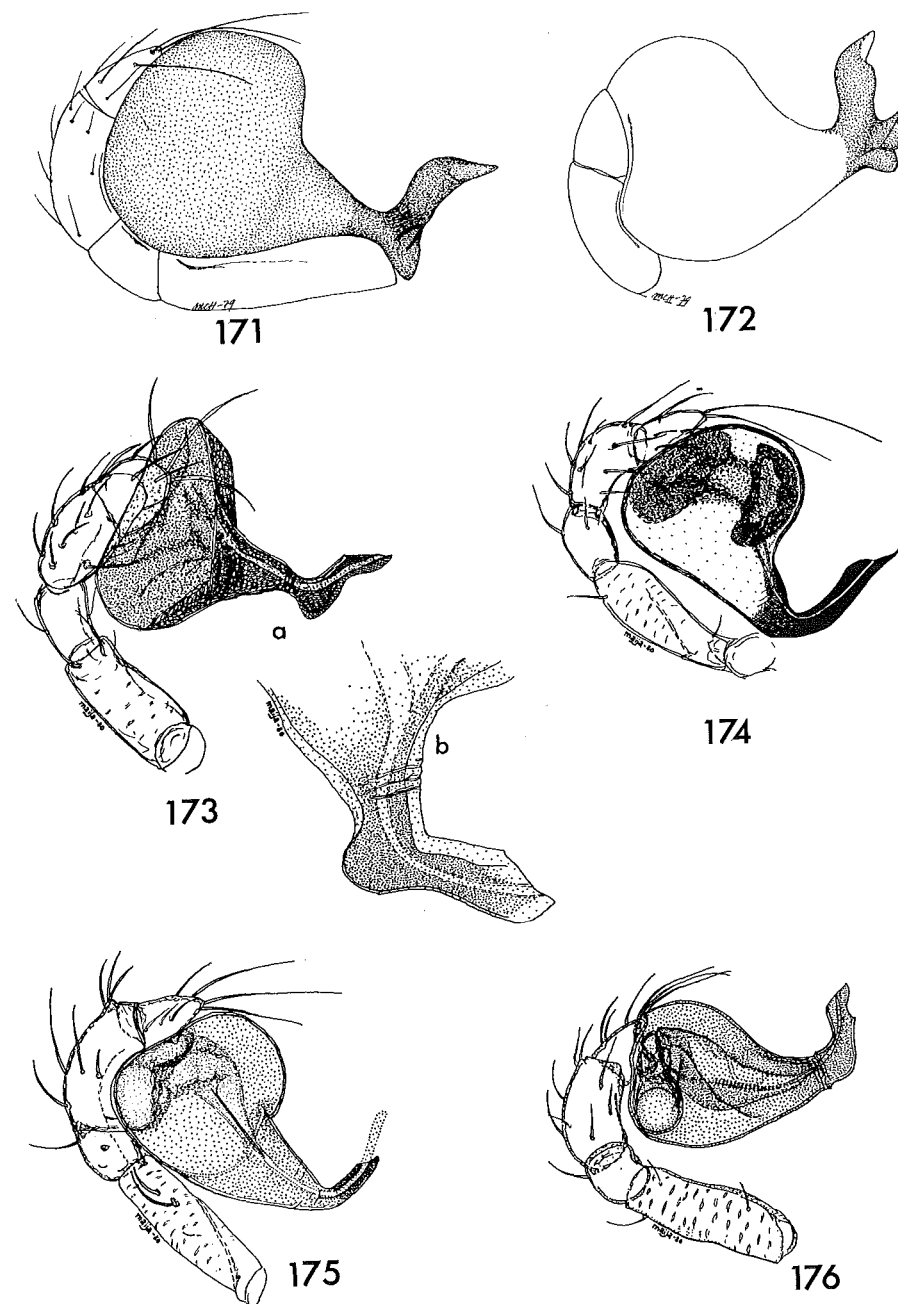
Figs. 149—148. *Ablemma (Bannia) k. kaindi* sp. n. (149, 151), *A. (B.) k. avios* ssp. n. (150), *A. (B.) circum-spectans* sp. n. (152), *A. (B.) ruohomaekii* sp. n. (153), *A. (B.) erna* sp. n. (154), and *A. (B.) lempake* sp. n. — 149, 150, 152, 154: male carapace laterally. — 151, 153: female sternum ventrally. — 155: female carapace laterally.



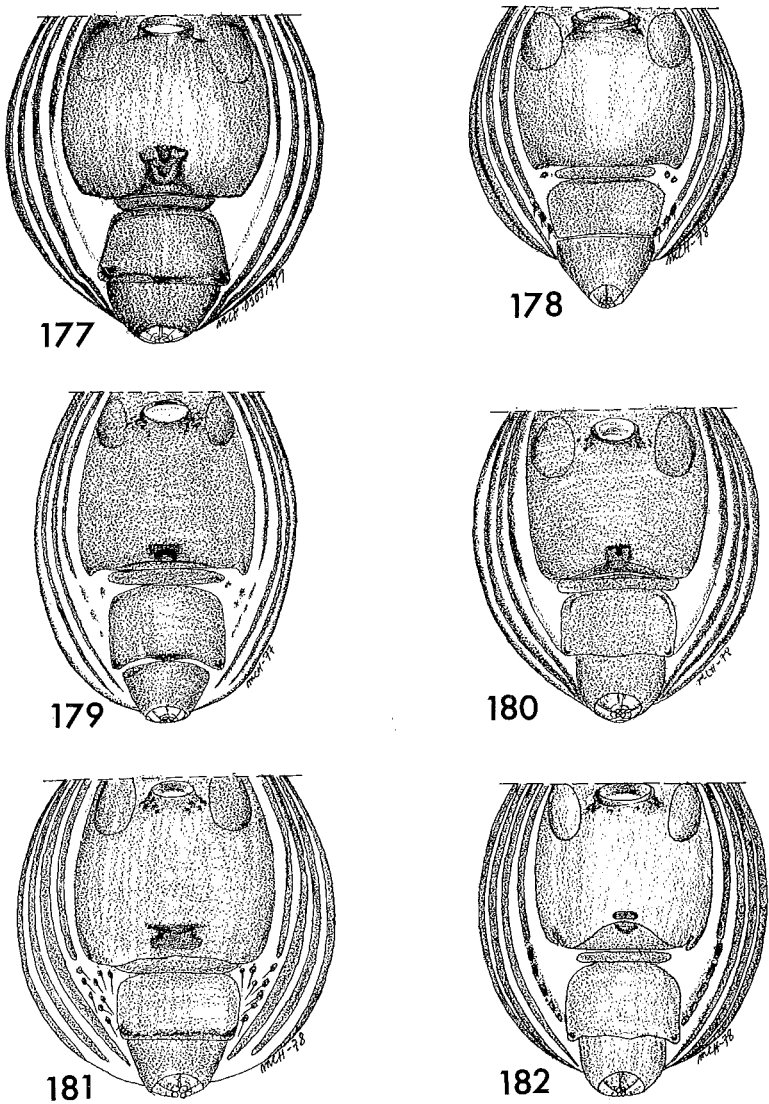
Figs 156—163. *Ablemma (Bannia) girinum* sp. n. (holotype) (156), *A. (B.) singalang* sp. n. (157), *A. (B.) datahu* sp. n. (158, 162), *A. (B.) samarinda* sp. n. (159), *A. (B.) lempake* sp. n. (160), and *A. (B.) merotai* sp. n. (holotype) (161, 163). — 156—161: male carapace. — 162—163: male chelicerae.



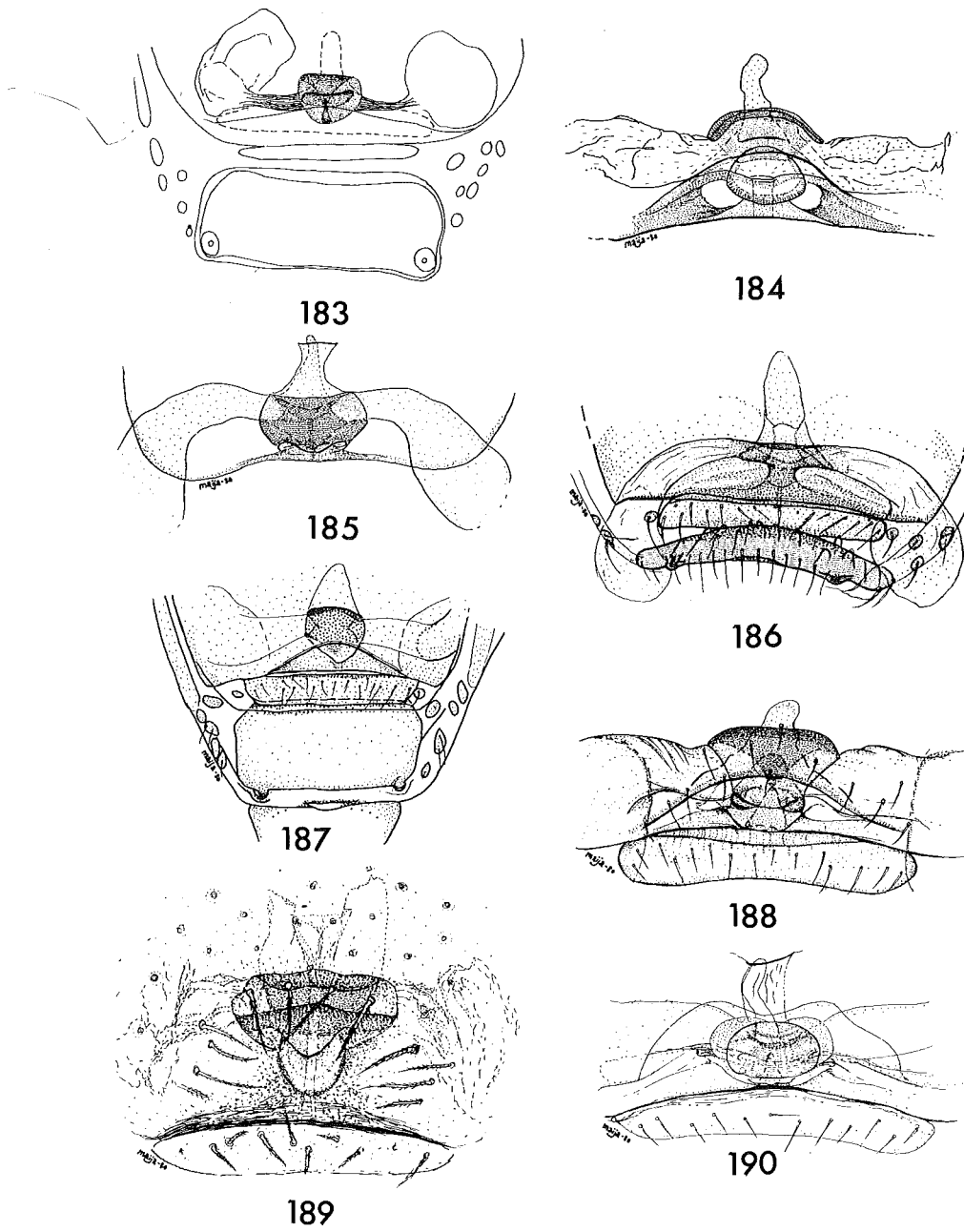
Figs 164—170. *Ablemma (Bannia) k. kaindi* sp. n. (164), *A. (B.) circumspectans* Deeleman-Reinhold (165), *A. (B.) kaindi avios* sp. n. (holotype) (166), *A. (B.) ruohomaekii* sp. n. (167), *A. (B.) girinum* sp. n. (holotype) (169), and *A. (B.) singalang* sp. n. (170). — 164—170: male palp.



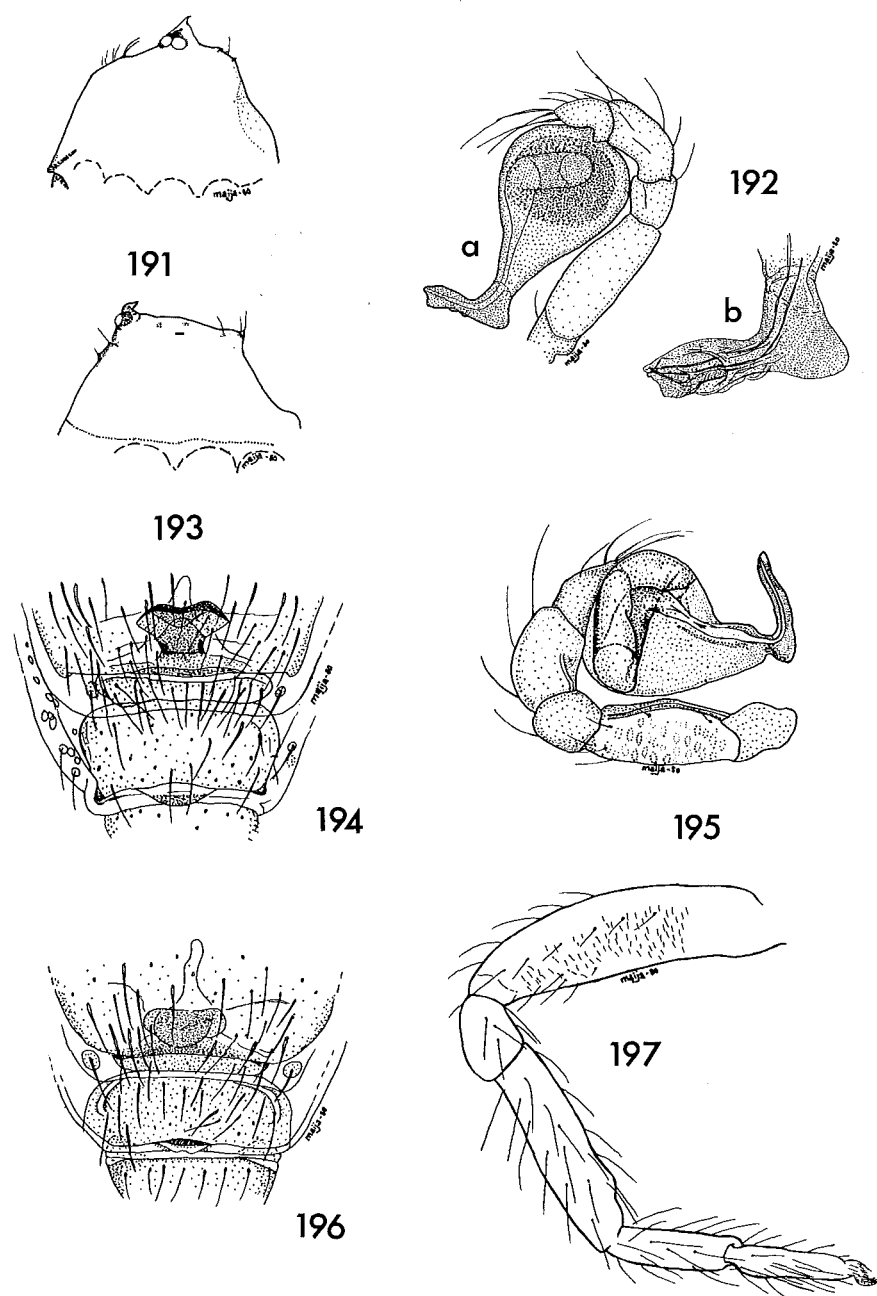
Figs 171—176. *Ablemma (Bannia) erna* sp. n. (171—172), *A. (B.) merotai* sp. n. (173), *A. (B.) lempake* sp. n. (174), *A. (B.) samarinda* sp. n. (175), and *A. (B.) datahu* sp. n. (176). — 171: male palp laterally. — 172: male palp mesially. — 173: male palp laterally, (a) with bulbus slightly distorted and (b) embolus (holotype). — 175—176: male palp laterally.



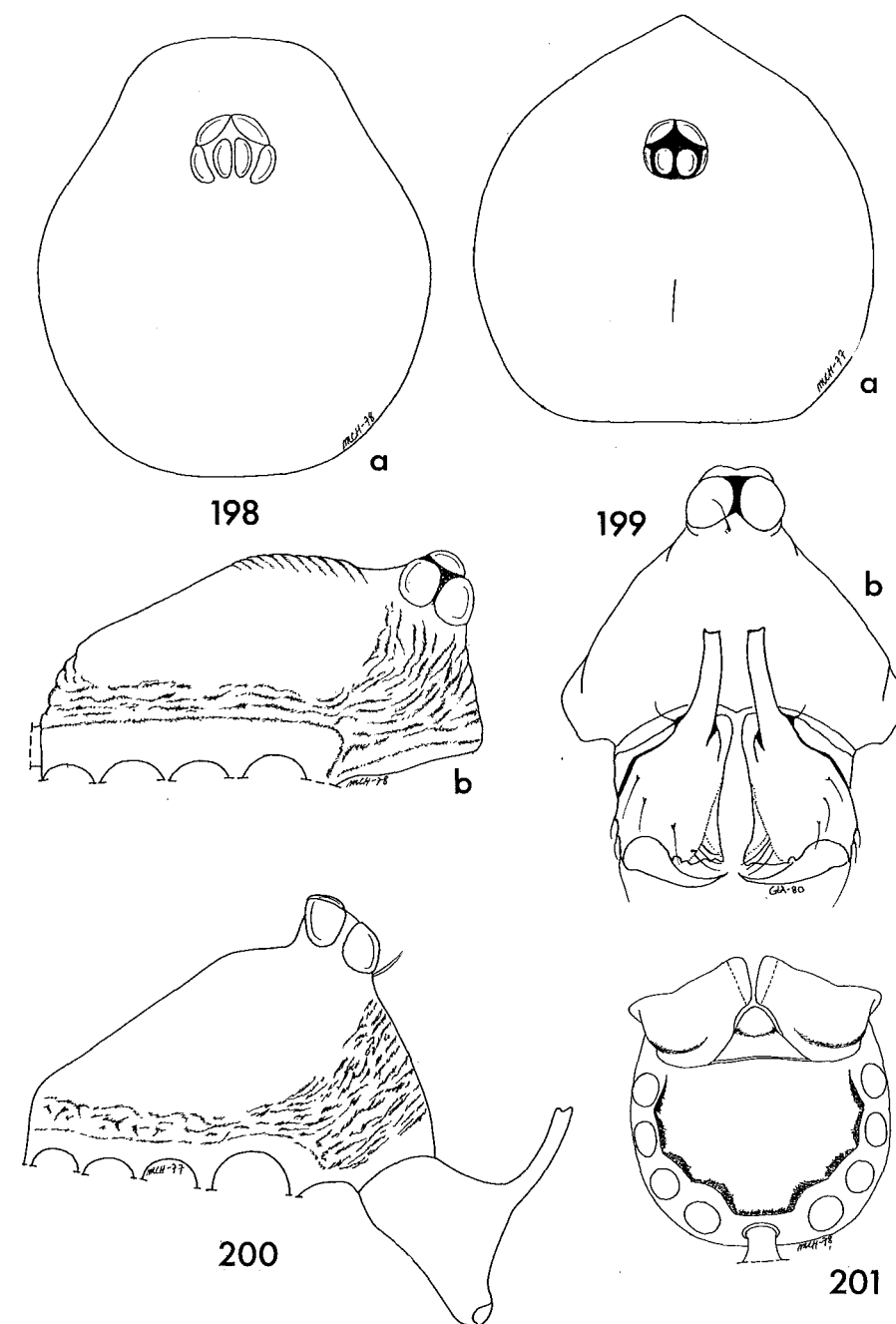
Figs 177—182. *Ablemma (Bannia) erna* sp. n. (177), *A. (B.) k. kaindi* sp. n. (178, 180), *A. (B.) kaindi avios* ssp. n. (179), *A. (B.) circumspectans* Deeleman-Reinhold (181), and *A. (B.) pugnax* (Brignoli) (182). — 177, 179—182: female abdomen ventrally. — 178: male abdomen ventrally.



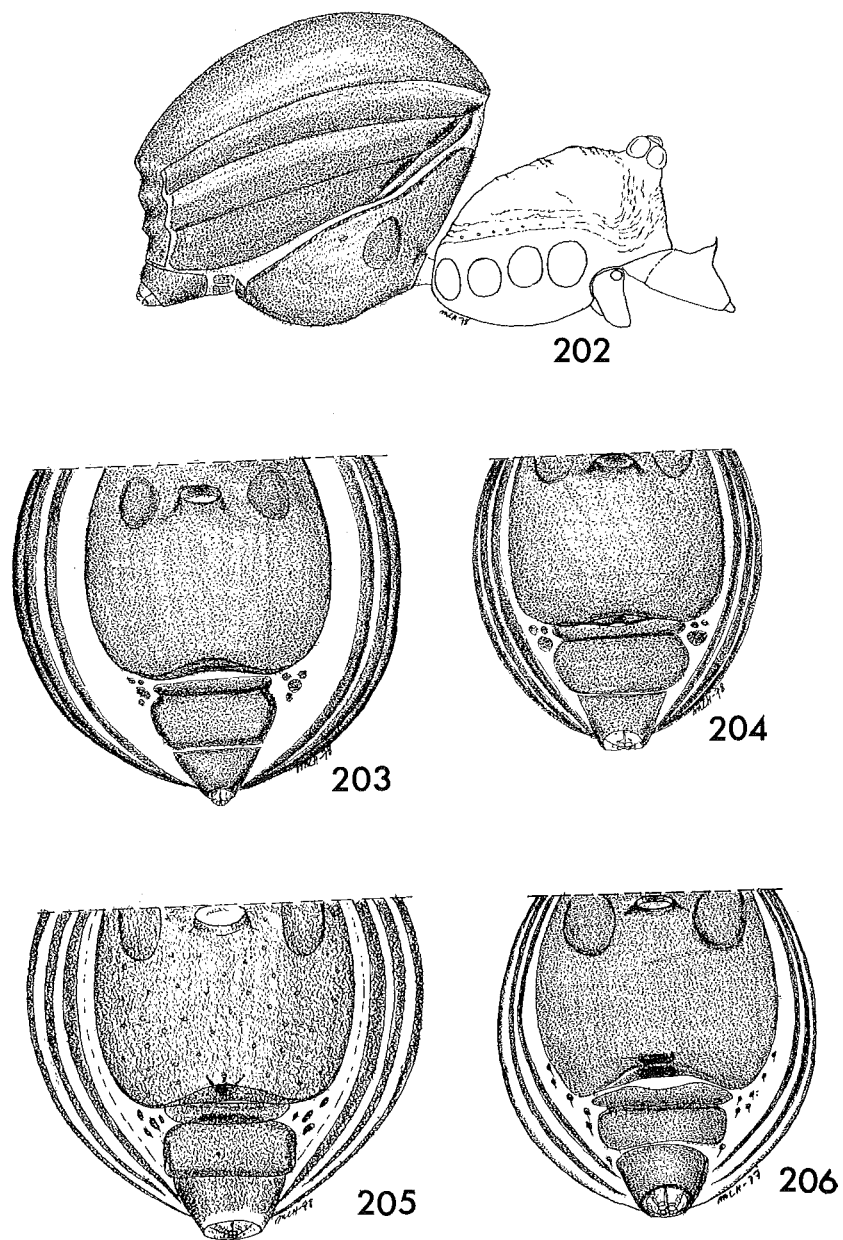
Figs 183—190. *Ablemma (Bannia) k. kaindi* sp. n. (183), *A. (B.) pugnax* (Brignoli) (184), *A. (B.) circumspectans* Deeleman-Reinhold (185), *A. (B.) syahdani* sp. n. (holotype) (186), *A. (B.) makiling* sp. n. (187), *A. (B.) lempake* sp. n. (188), *A. (B.) erna* sp. n. (189), and *A. (B.) datahu* sp. n. (190). — 183—190: epigynal area with cleared vulva.



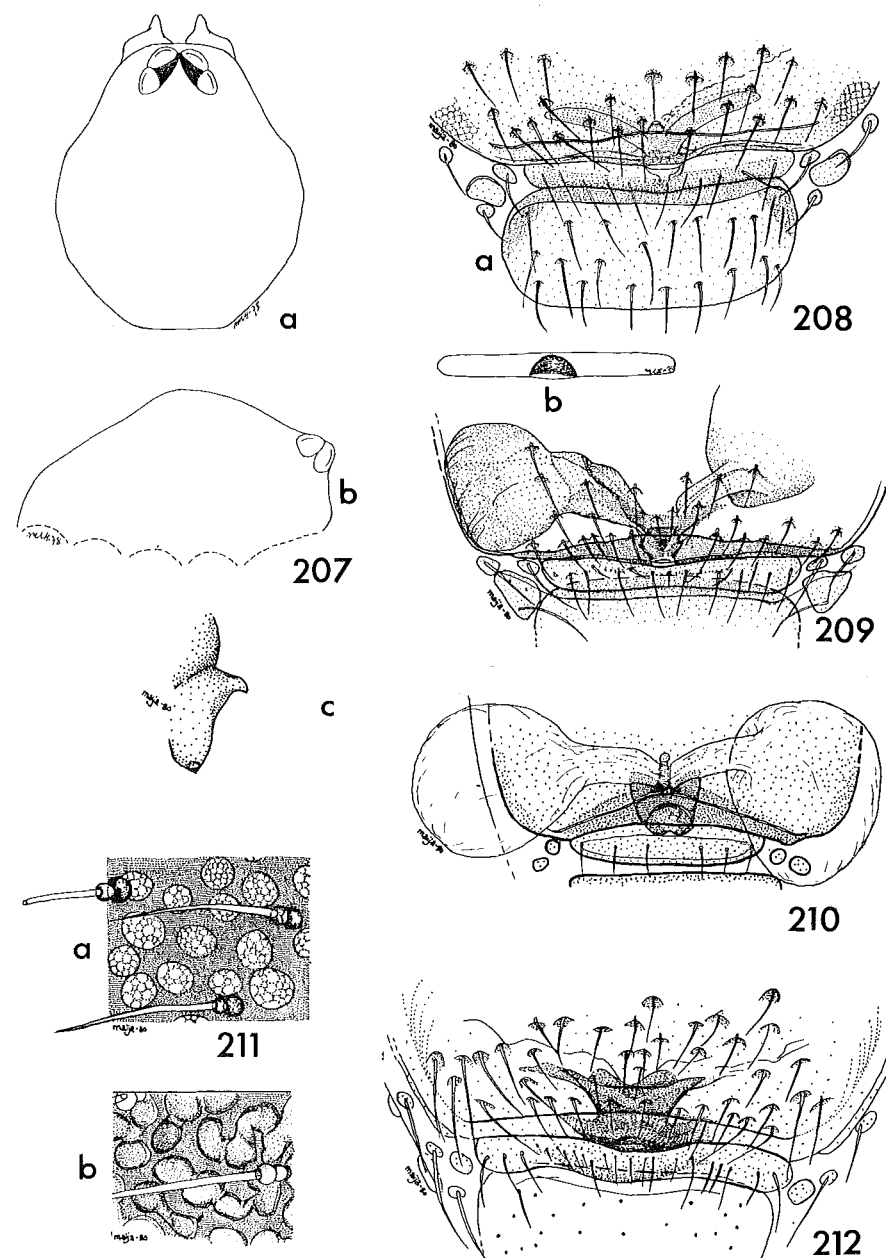
Figs 191—197. *Ablemma (Bannia) makiling* sp. n. (191—192), *A. (B.) rarosae* sp. n. (193, 195), *A. (B.) lempake* sp. n. (194), *A. (B.) datahu* sp. n. (196), *A. (B.) k. kaindi* sp. n. (197). — 191, 193: male carapace laterally (holotypes). — 192: (a) male palp mesially and (b) embolus. — 194, 196: epigynal area and preanal plate. — 195: male palp laterally. — 197: leg I of male.



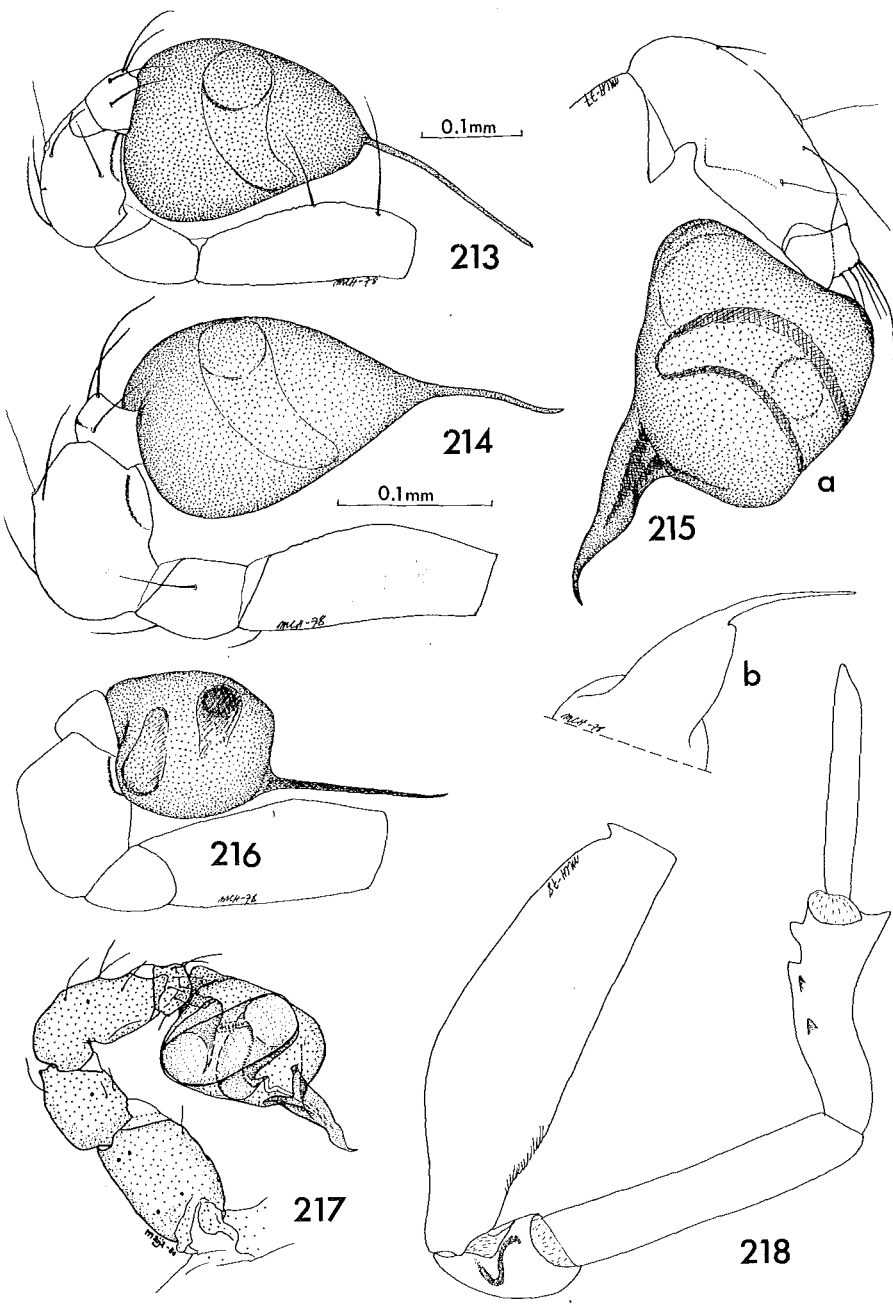
Figs 198—201. *Shearella lilawati* sp. n. (198) and *Gunasekara ramboda* sp. n. (199—201). — 198a, 199a: male carapace dorsally. — 198b: male carapace laterally. — 199b: male clypeus and chelicerae frontally. — 200: male carapace and chelicerae laterally. — 201: male gnathocoxae, labium, and sternum.



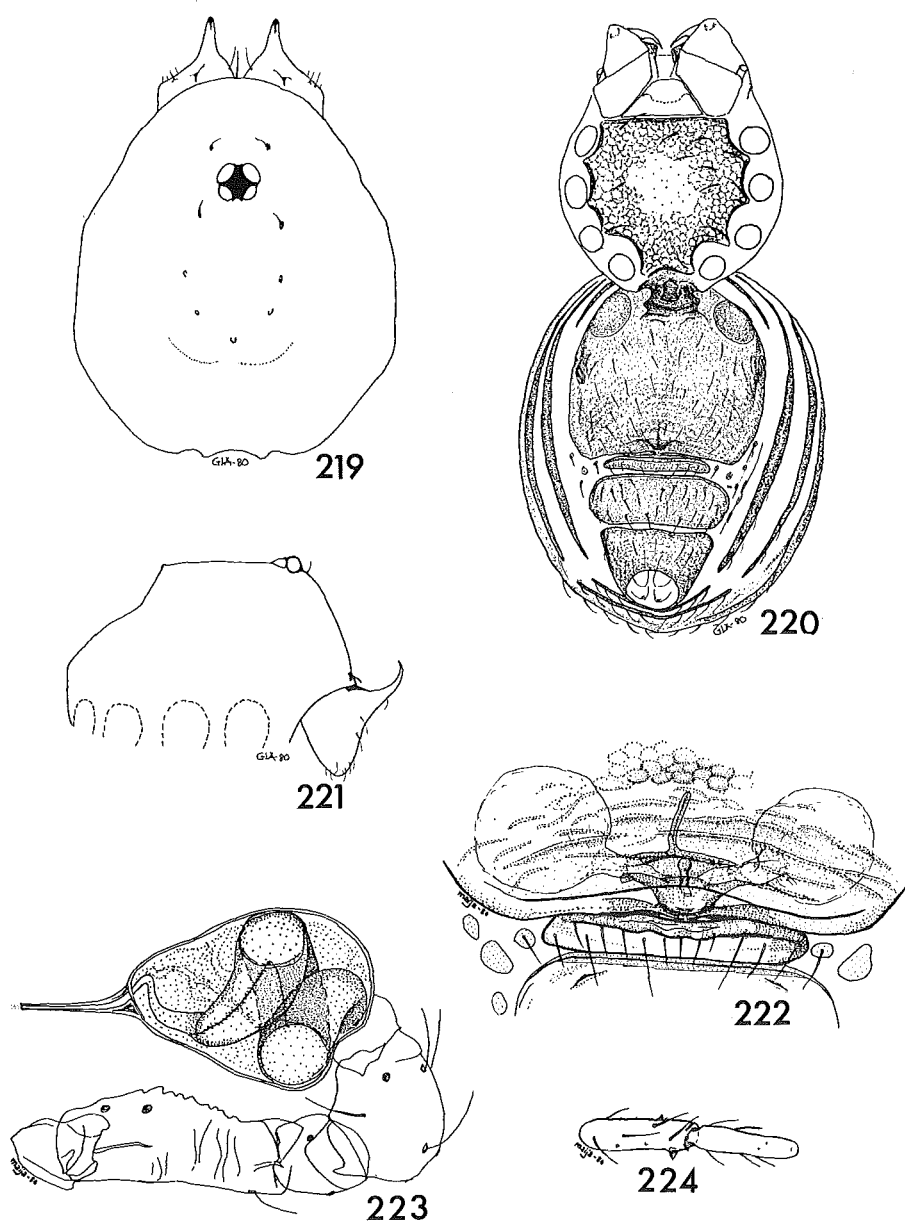
Figs 202—206. *Shearella lilawati* sp. n. (202—203), *S. selvarani* sp. n. (204), *Mariblemma pandani* (Brignoli) (205), and *Gunasekara ramboda* sp. n. (206). — 202: male carapace and abdomen laterally. — 203—206: female abdomen ventrally.



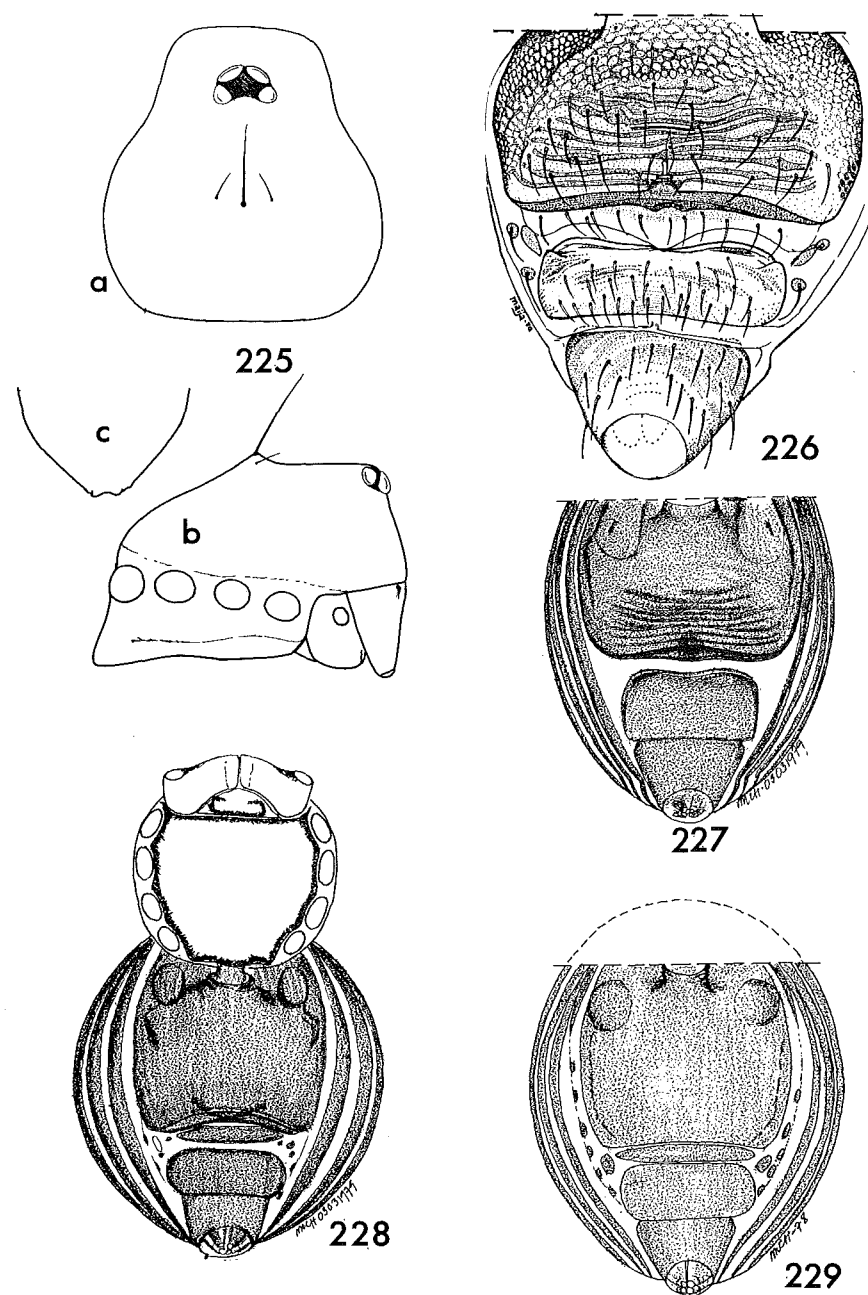
Figs 207—212. *Mariblemma pandani* (Brignoli) (207, 210, 211a), *Shearella lilawati* sp. n. (208), *S. selvarani* sp. n. (209), and *Gunasekara ramboda* sp. n. (211b, 212). — 207: (a) male carapace dorsally, (b) male carapace laterally, and (c) male chelicera laterally. — 208: (a) female epigynal area and cleared vulva and (b) inner vulva plate. — 209—210, 212: epigynal area and cleared vulva. — 211: surface of sternum.



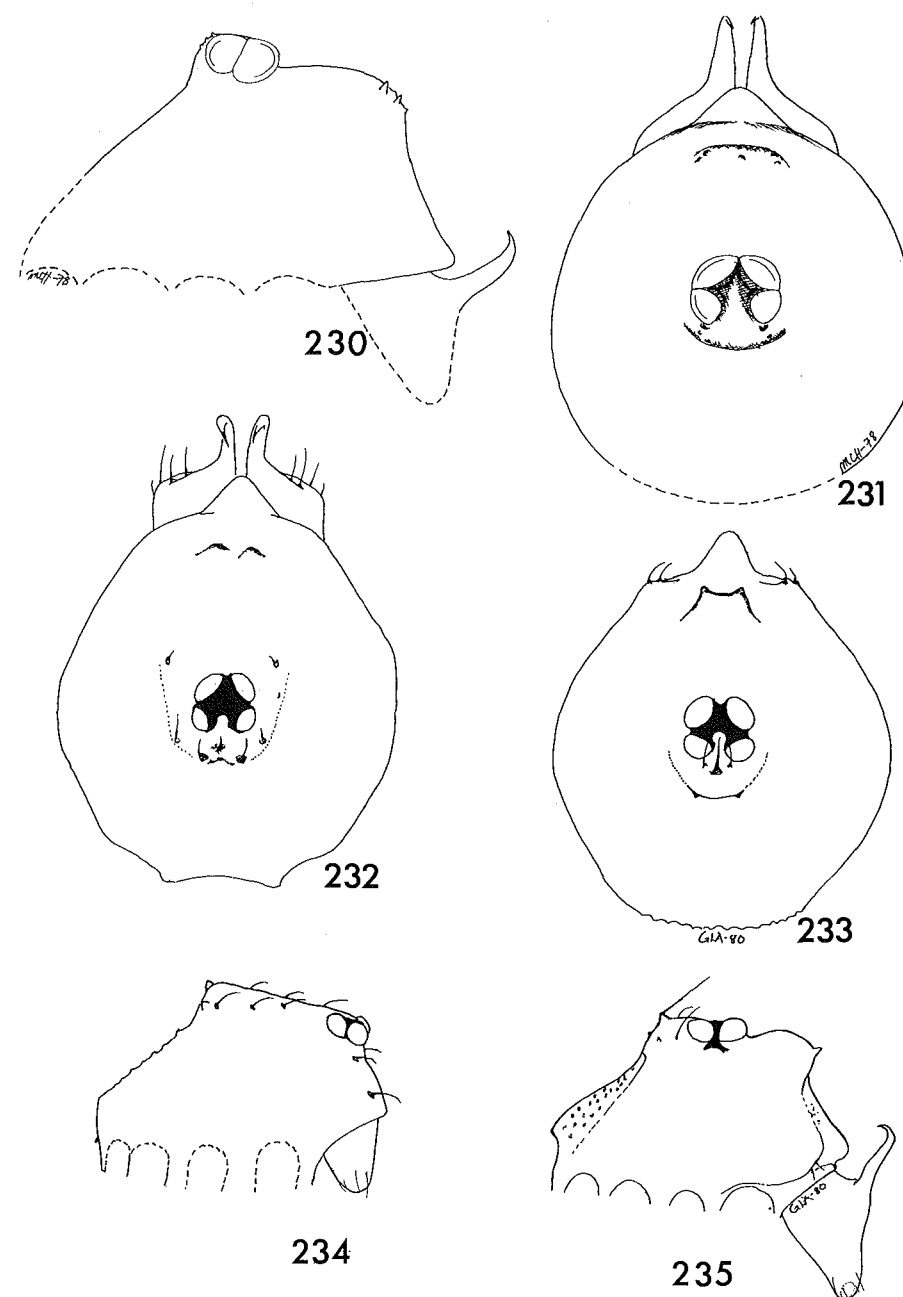
Figs 213—218. *Shearella selvarani* sp. n. (213), *S. lilawati* sp. n. (214), *Gunasekara ramboda* sp. n. (215, 217—218), and *Mariblemma pandani* (Brignoli) (216). — 213—214: male palp. — 215: (a) male palp and (b) embolus mesially. — 216—217: male palp laterally. — 218: leg I of male.



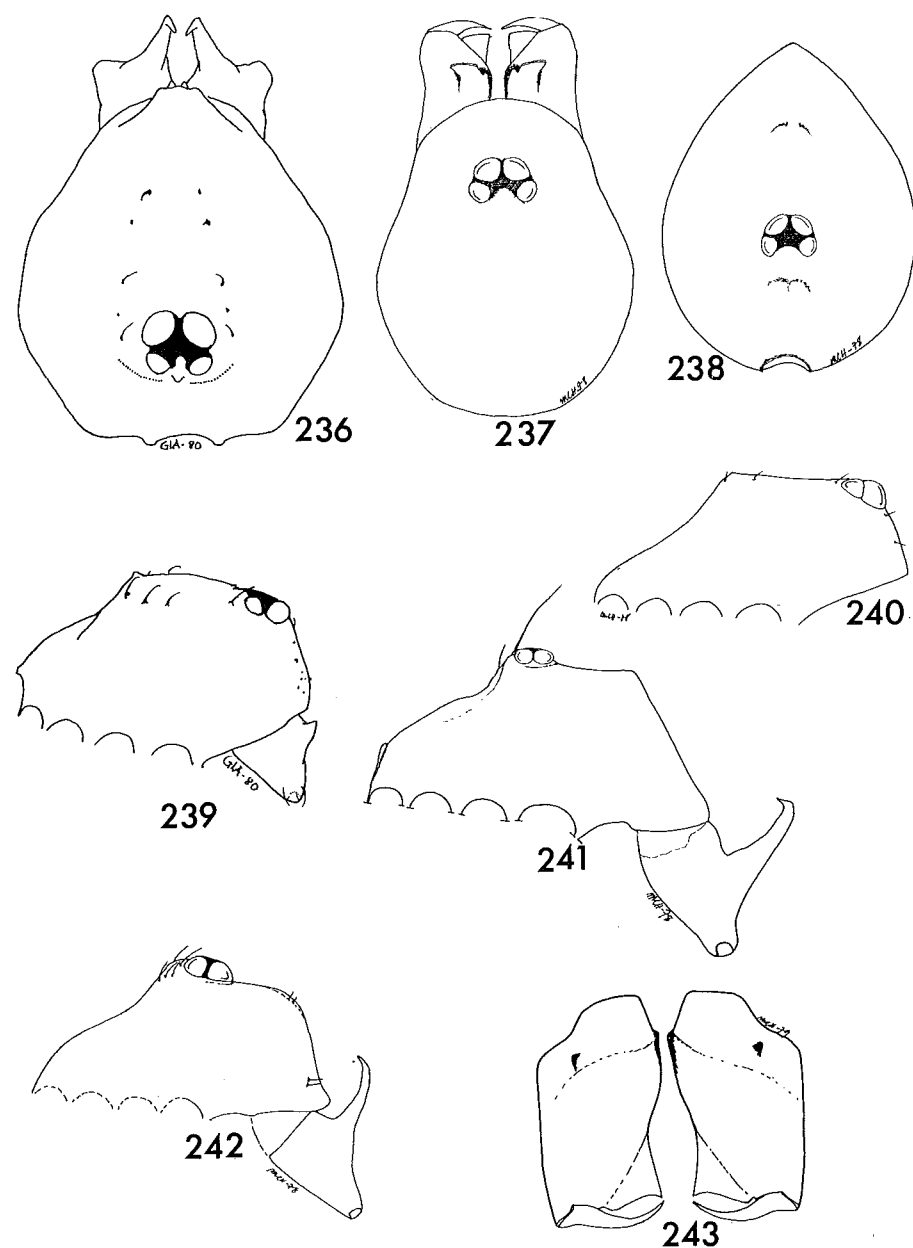
Figs 219—224. *Tetrablemma (Kumaonia) loebli* Bourne. — 219: male carapace dorsally. — 220: female abdomen and carapace ventrally. — 221: male carapace laterally. — 222: epigynal area and cleared vulva. — 223: male palp. — 224: leg I of male dorsally (metatarsus with modifications and tarsus).



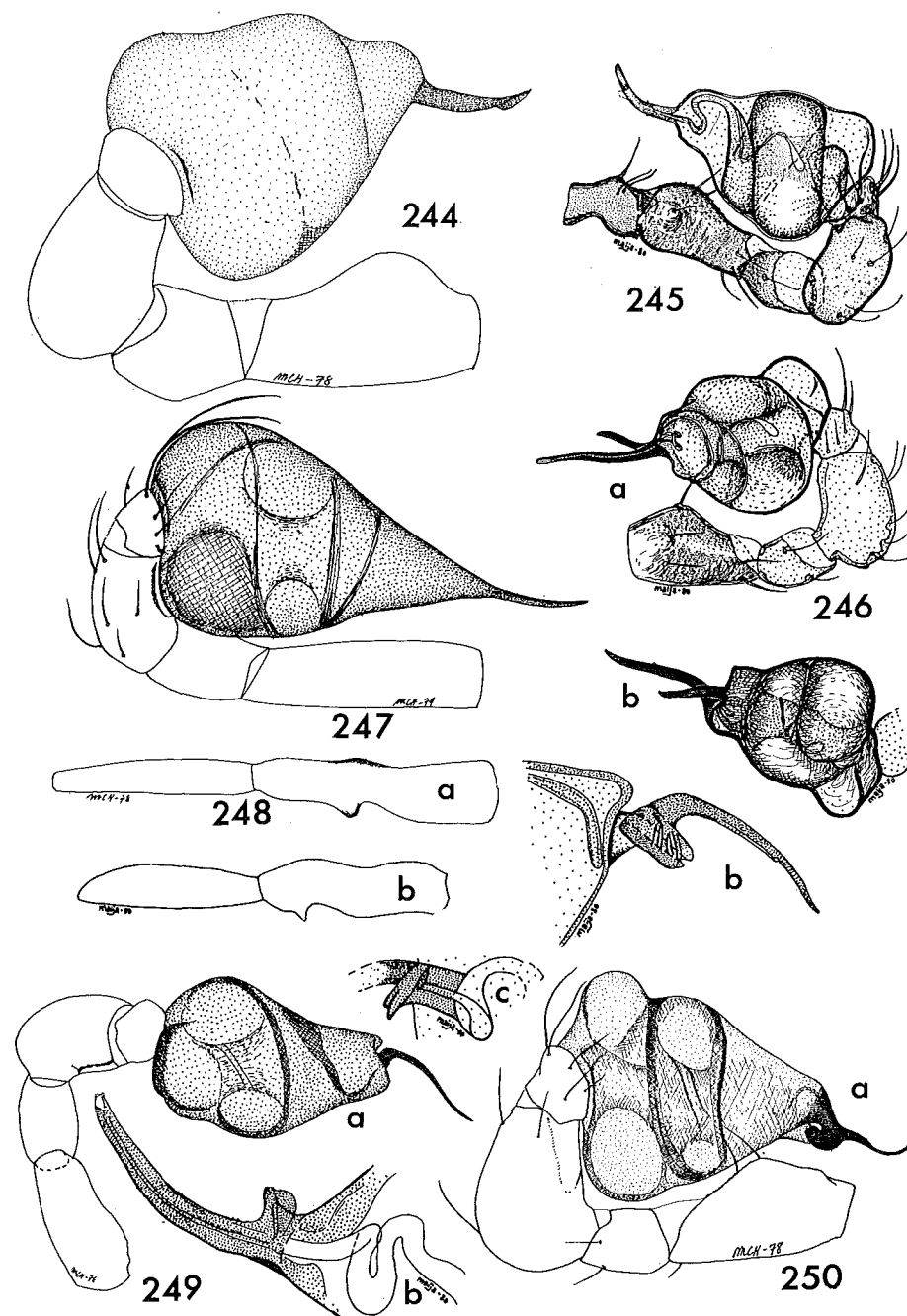
Figs 225—229. *Singalangia sternalis* sp. n. (225—227), *Tetrablemma (Indonops) benoiti* (Brignoli) (228), and *T. (T.) m. medioculatum* O. Pickard-Cambridge (229). — 225: (a) female carapace dorsally, (b) sternum and carapace laterally and (c) apex of sternum ventrally. — 226: epigynal area and cleared vulva. — 227: female abdomen ventrally. — 228: female sternum and abdomen ventrally. — 229: male abdomen ventrally (holotype).



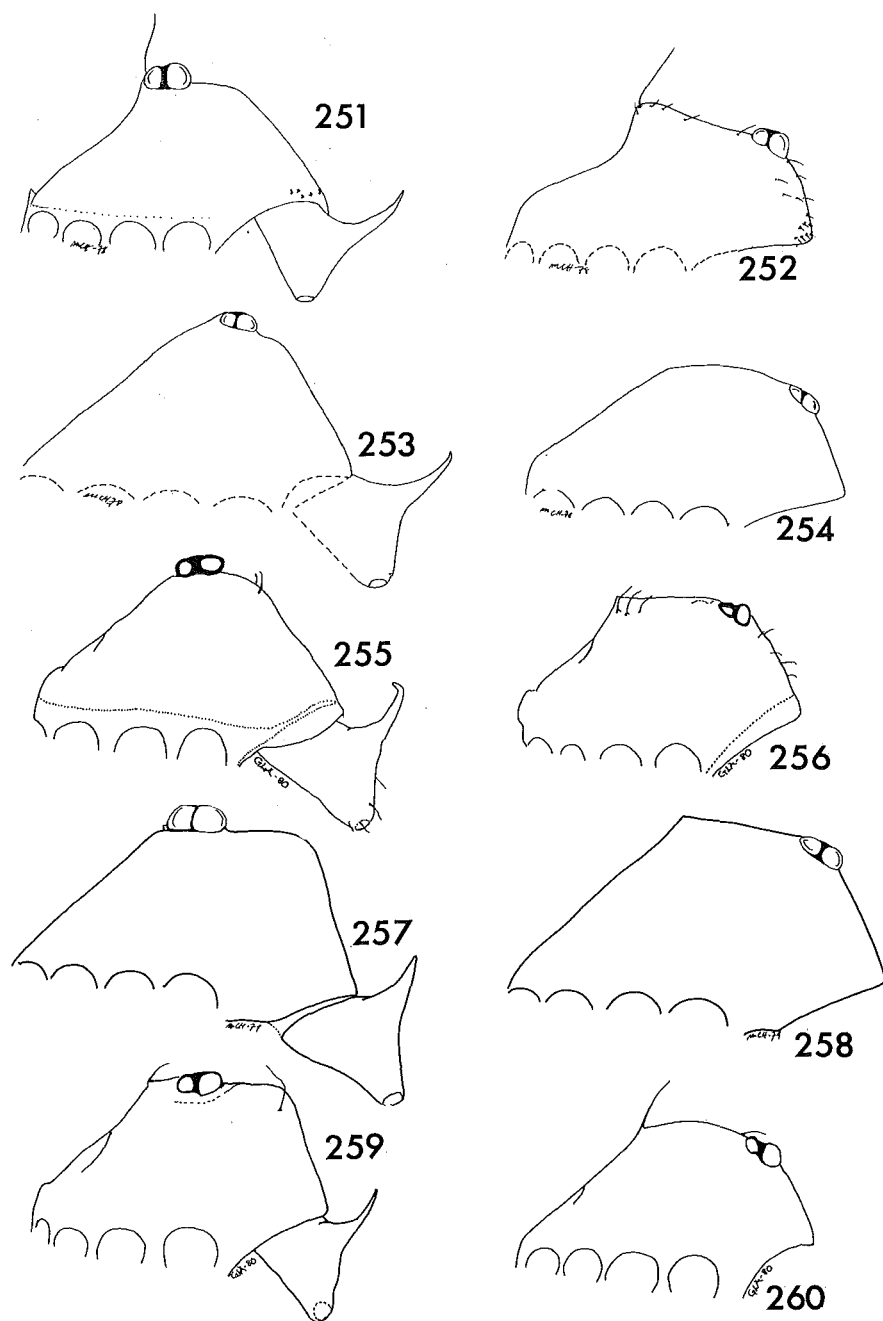
Figs 230—235. *Tetrablemma (T.) medioculatum* O. Pickard-Cambridge: ssp. *medioculatum* (holotype) (230—231), ssp. *gangeticum* ssp. n. (232, 234), and ssp. *cochinense* ssp. n. (233, 235). — 230, 235: mte carapace laterally. — 231—233: male carapace dorsally. — 234: female carapace laterally.



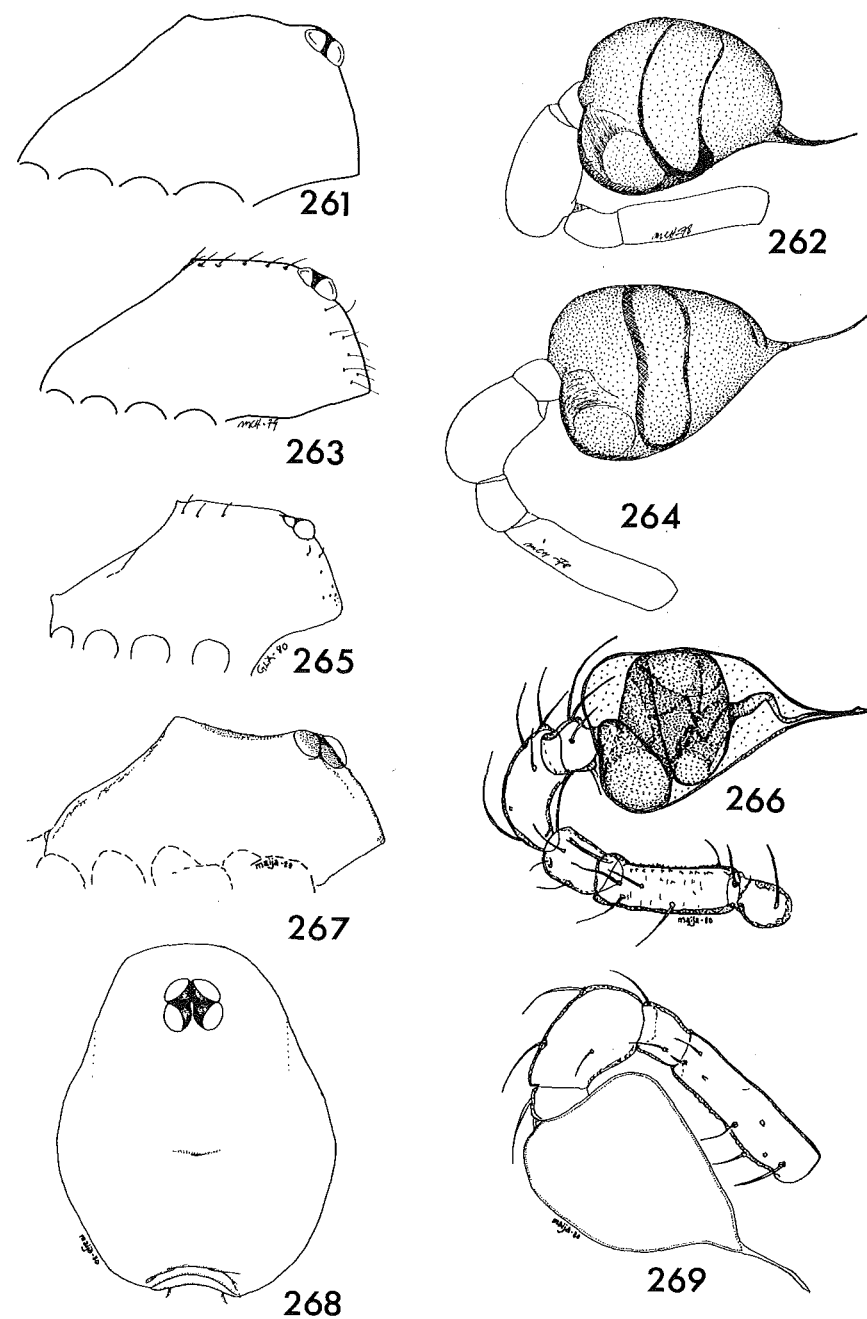
Figs 236–243. *Tetrablemma* (*T.*) *brignolii* sp. n. (236, 239), *T.* (*T.*) *okei* Butler (237–238, 240–241), *T.* (*T.*) *rhinoceros* (Brignoli) (242), and *T.* (*Indonops*) *mardionoi* sp. n. (243). — 236: male carapace and chelicerae. — 237: female carapace and chelicerae. — 238: male carapace. — 239: female carapace and chelicerae (intersexual specimen). — 240: female carapace. — 241–242: male carapace and chelicerae laterally. — 243: female chelicerae.



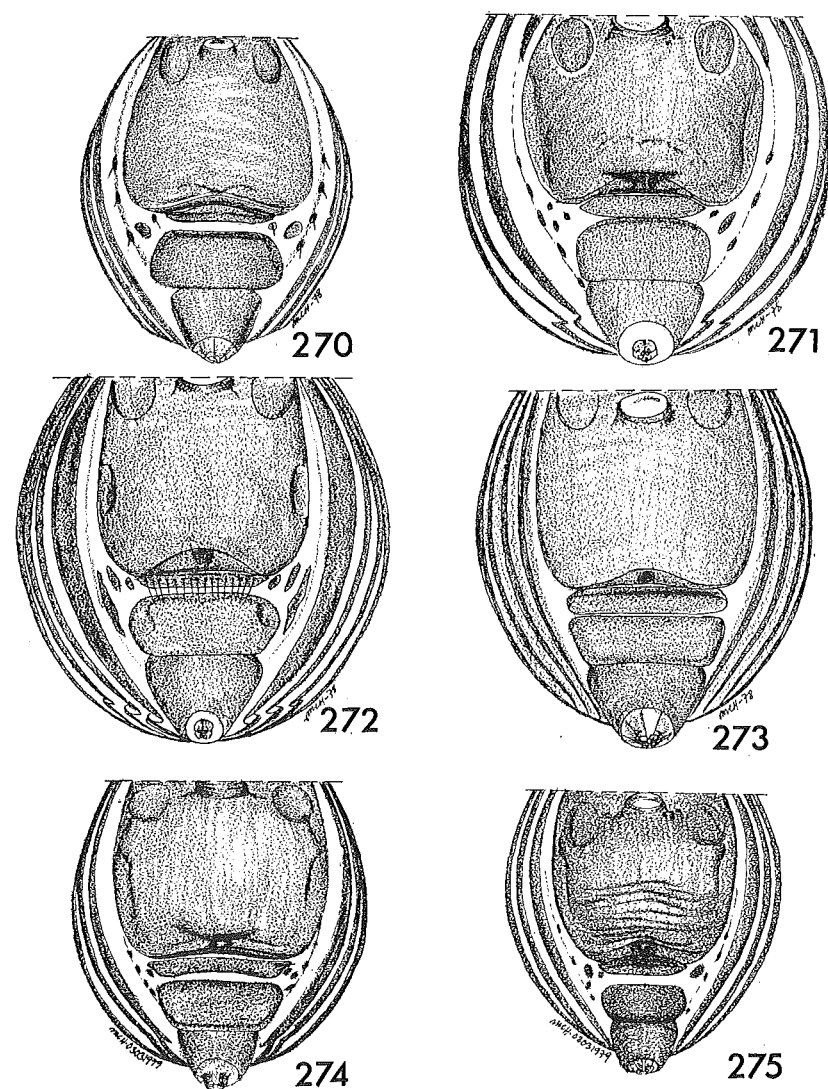
Figs 244–250. *Tetrablemma* (*T.*) *m. medioculatum* O. Pickard-Cambridge (244), *T.* (*T.*) *m. gangeticum* ssp. n. (245), *T.* (*T.*) *brignolii* sp. n. (246), *T.* (*Indonops*) *mardionoi* sp. n. (247), *T.* (*T.*) *okei* Butler (248a, 250), and *T.* (*T.*) *rhinoceros* (Brignoli) (248b, 250). — 244: male palp laterally. — 245: male palp mesially. — 246: (a) male palp mesially and (b) bulbus laterally. — 247: male palp laterally. — 248: leg I of male, tarsus and metatarsus. — 249: (a) male palp laterally and (b) embolus mesially. — 250: (a) male palp laterally, (b) embolus mesially, and (c) base of embolus laterally.



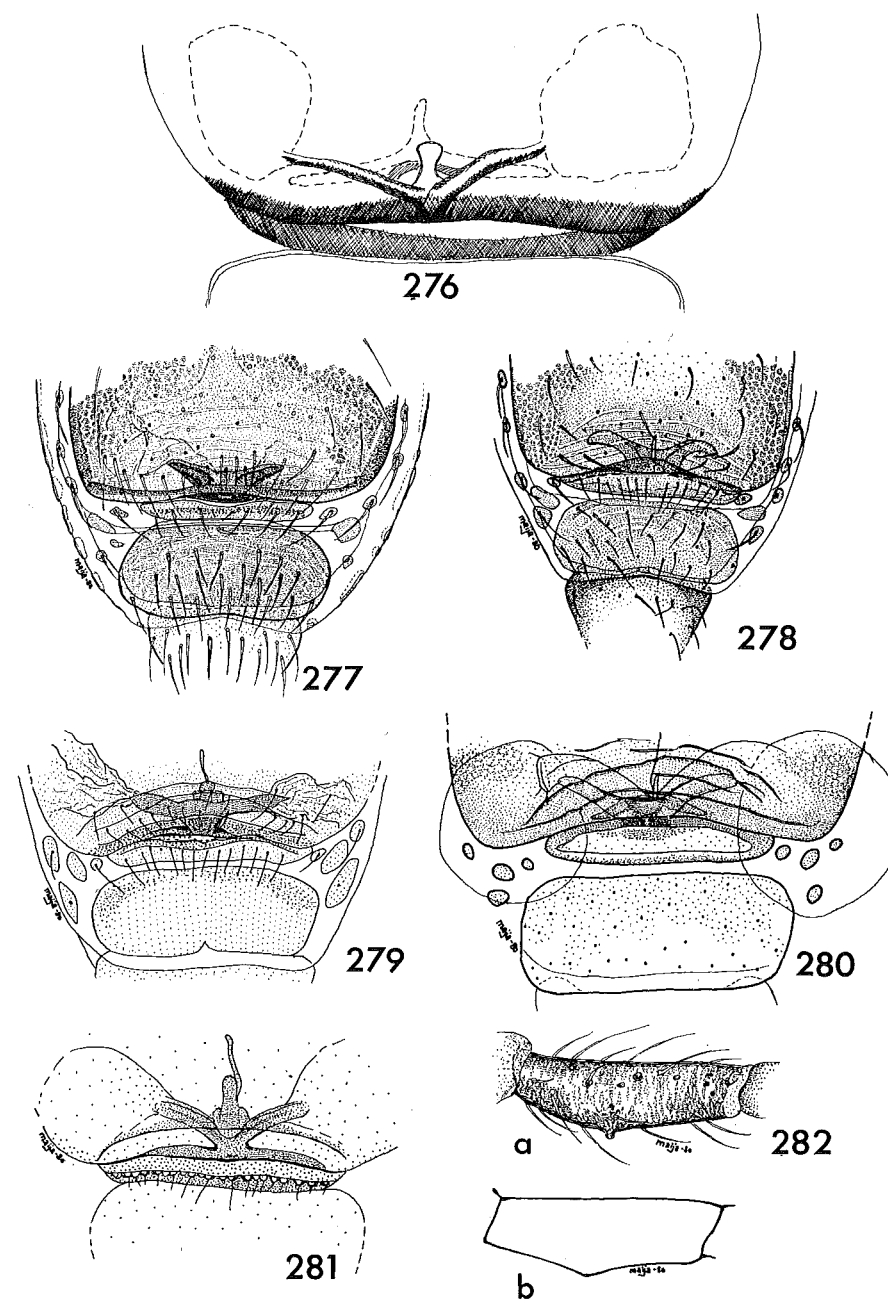
Figs 251–260. *Tetrablemma (Indonops) deccanensis* (Tikader) (251–252), *T. (I.) samoensis* Marples (253–254), *T. (I.) marawula* sp. n. (255–256), *T. (I.) mardionoi* sp. n. (257–258), and *T. (I.) manggarai* sp. n. (259–260). — 251, 253, 255, 257, 259: male carapace and chelicerae laterally. — 252, 254, 256, 258, 260: female carapace laterally.



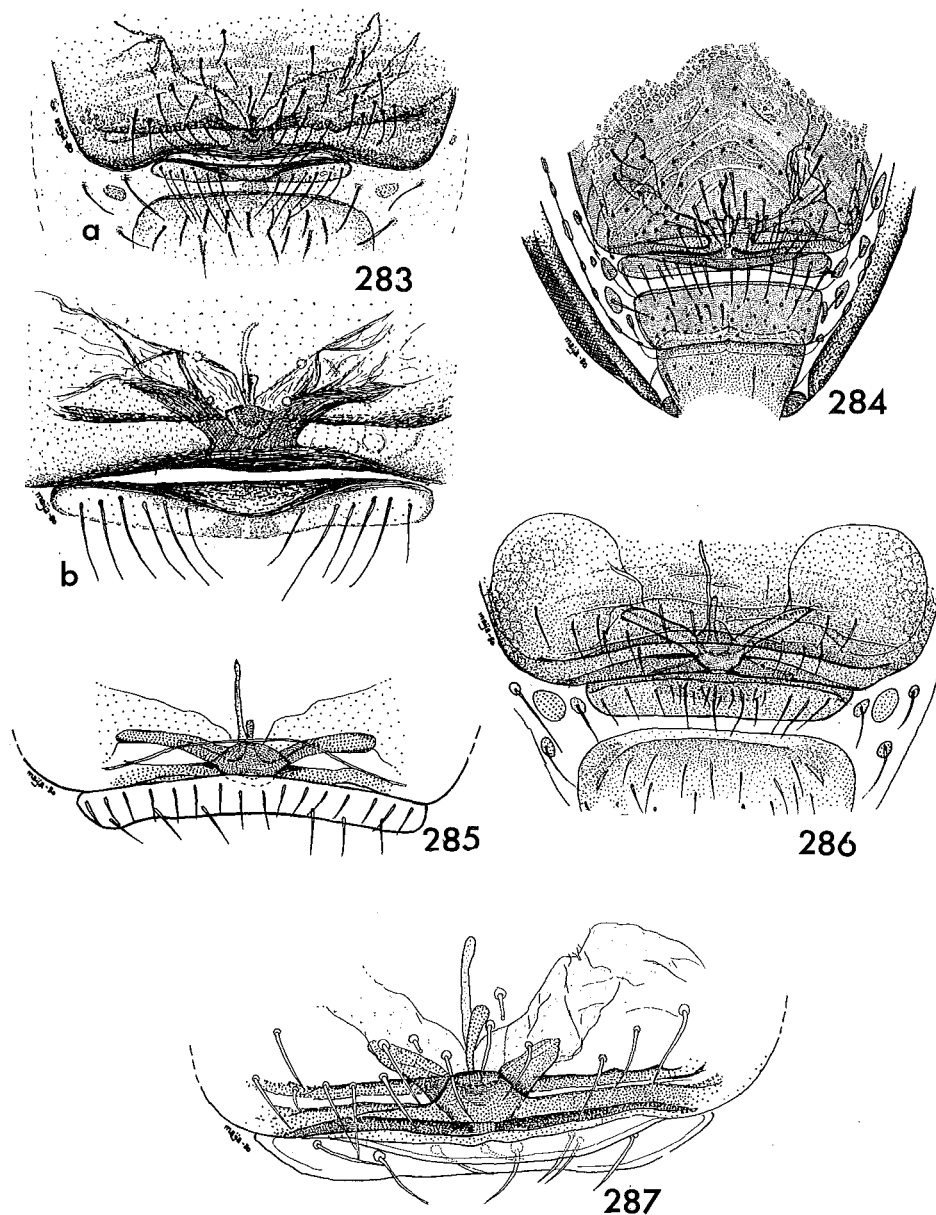
Figs 261–269. *Tetrablemma (Indonops) benoitii* (Brignoli) (261), *T. (I.) deccanensis* (Tikader) (262), *T. (I.) vietnamensis* sp. n. (263), *T. (I.) samoensis* Marples (264), *T. (I.) phulchoki* sp. n. (265), *T. (I.) marawula* sp. n. (266), *T. (I.) helenensis* Benoit (267–268), and *T. (I.) manggarai* sp. n. (269). — 261, 263, 265, 267: female carapace laterally. — 262, 264, 266, 269: male palp laterally. — 268: female carapace dorsally.



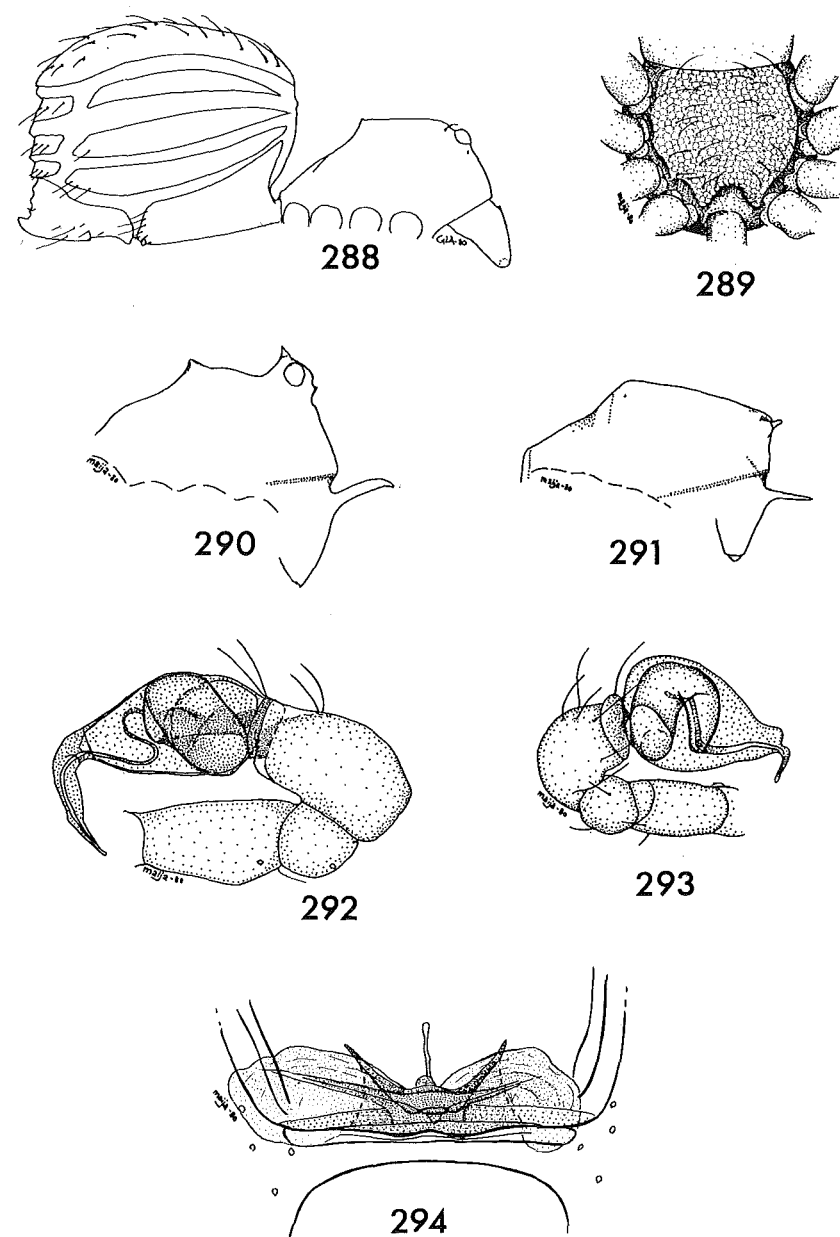
Figs 270—275. *Tetrablemma* (*T.*) *okei* Butler (270), *T. (T.) rhinoceros* (Brignoli) (271), *T. (Indonops) deccanensis* (Tikader) (272), *T. (I.) samoensis* Marples (273), *T. (I.) mardionoi* sp. n. (274), and *T. (I.) vietnamensis* sp. n. (275). — 270—275: female abdomen ventrally.



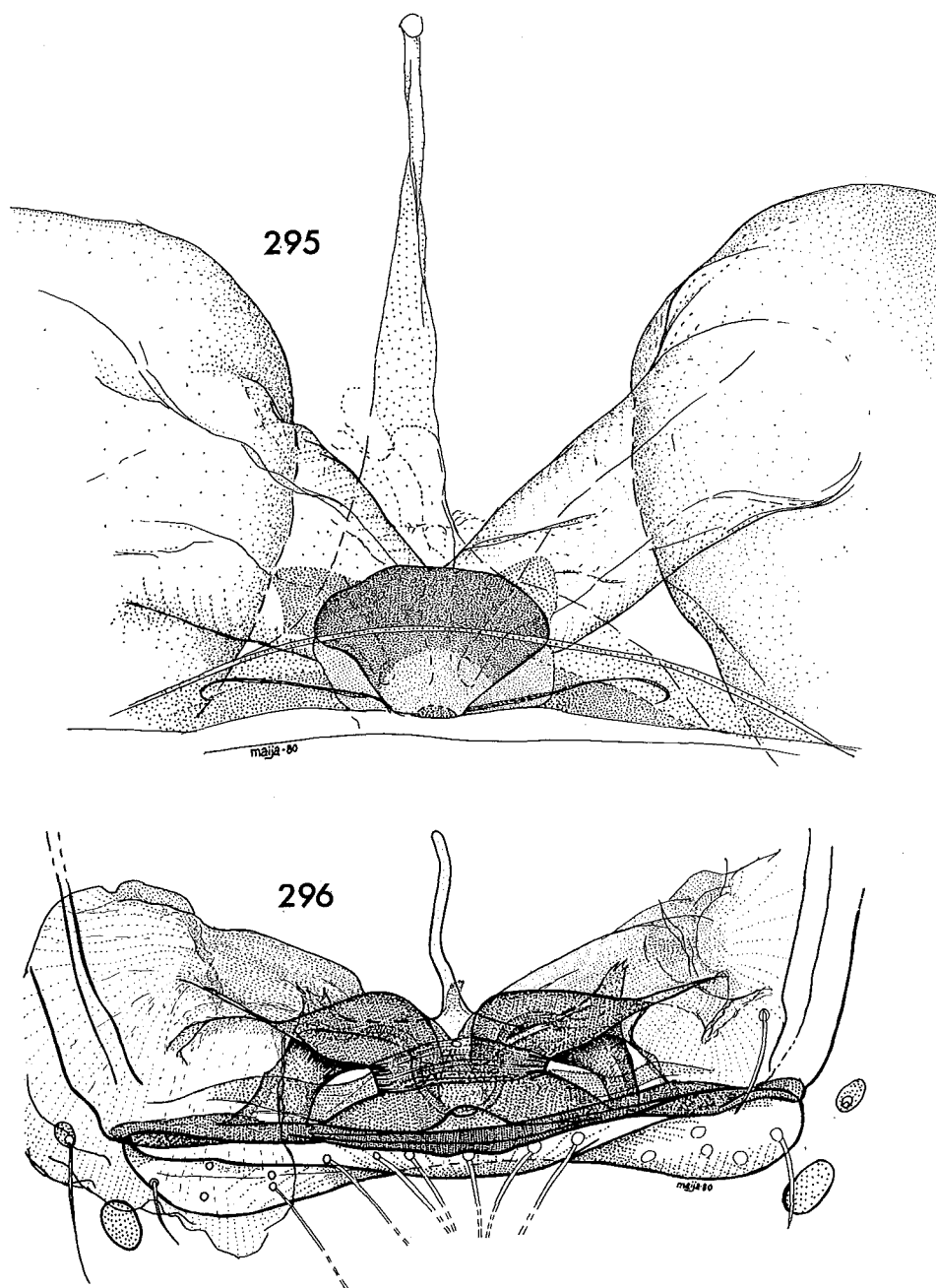
Figs 276—282. *Tetrablemma* (*T.*) *okei* Butler (276), *T. (T.) medioculatum gangeticum* spp. n. (277), *T. (T.) brignolii* sp. n. (278), *T. (Indonops) deccanensis* (Tikader) (279), *T. (I.) benoitii* (Brignoli) (280), *T. (I.) helenensis* Benoit (281), *T. (I.) manggarai* sp. n. (282a), and *T. (I.) mardionoi* sp. n. (282b). — 276: mounted vulva. — 277—281: epigynal area and cleared vulva. — 282: male tibia I laterally.



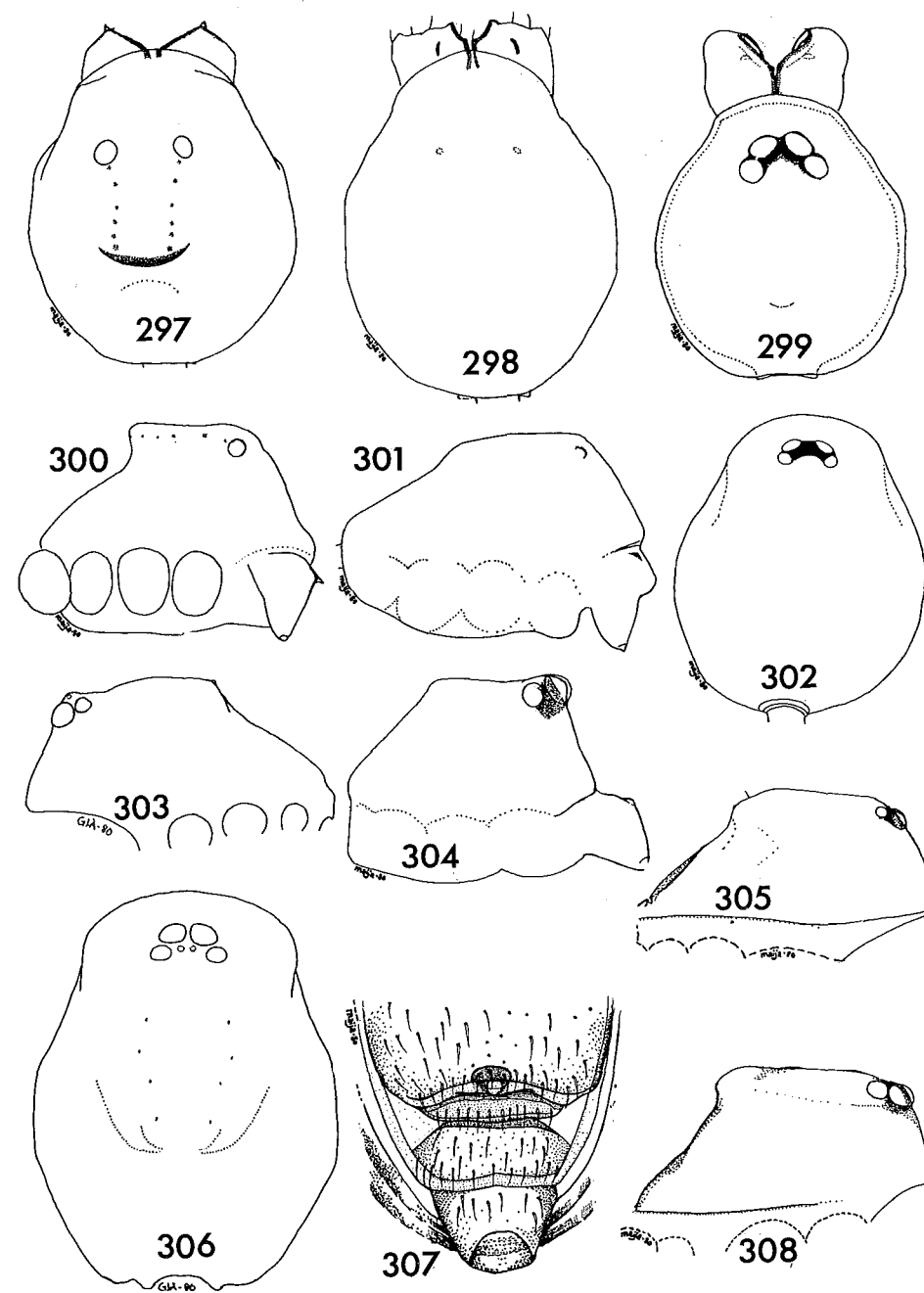
Figs 283—287. *Tetrablemma (Indonops) marawula* sp. n. (283), *T. (I.) phulchoki* sp. n. *T. (I.) mardionoi* sp. n. (285), *T. (I.) vietnamensis* sp. n. (286), and *T. (I.) mangarai* sp. n. (287). — 283: (a) epigynal area and cleared vulva and (b) central parts of vulva. — 284—287: epigynal area and cleared vulva.



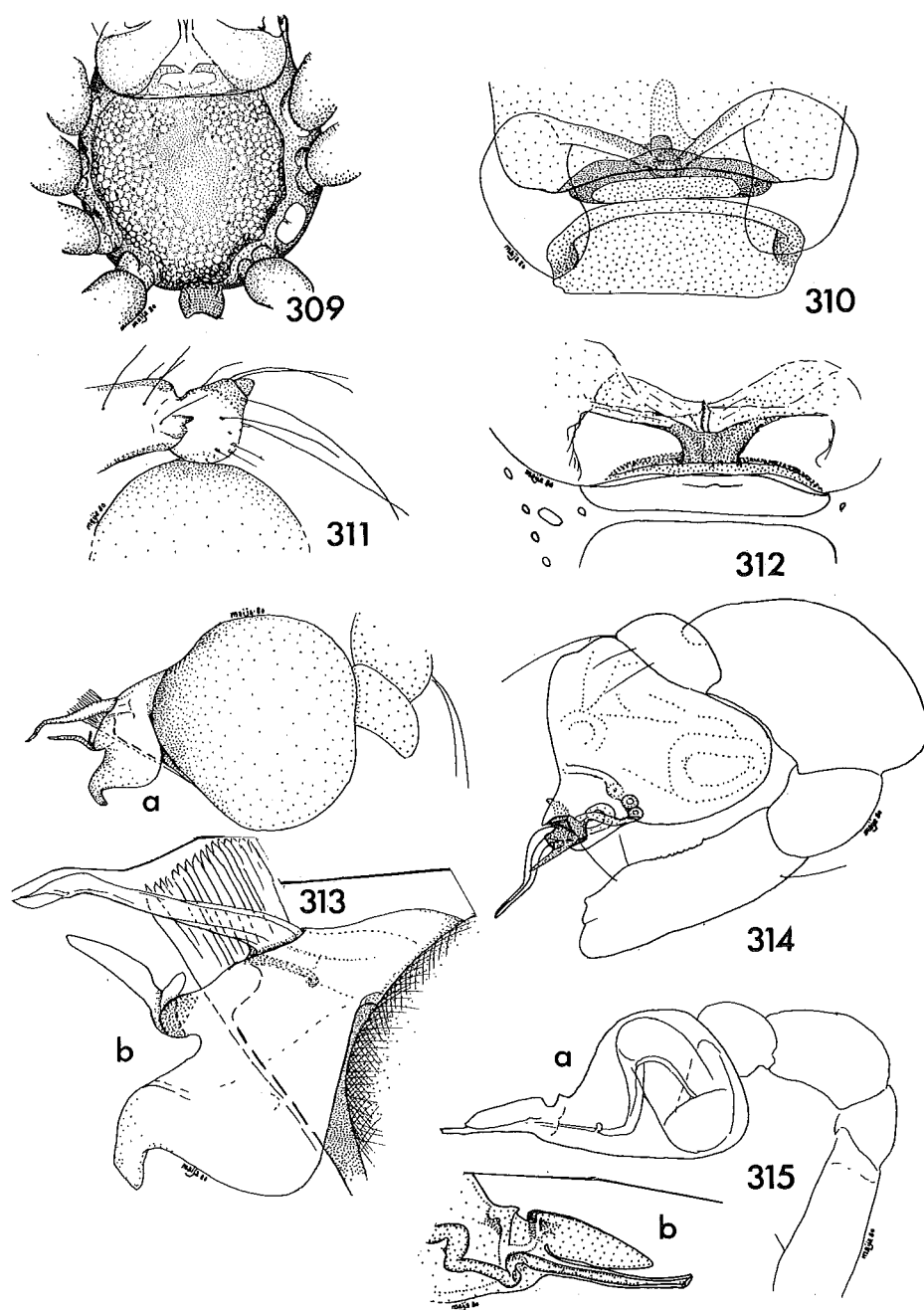
Figs 288—294. *Anansia astaroth* (Brignoli) (288—290, 292) and *Cuangoblemma machadoi* Brignoli (291, 293—294). — 288: female carapace and abdomen laterally. — 289: female sternum — 290—291: male carapace and chelicera laterally. — 292—293: male palp. — 294: epigynal area and cleared vulva.



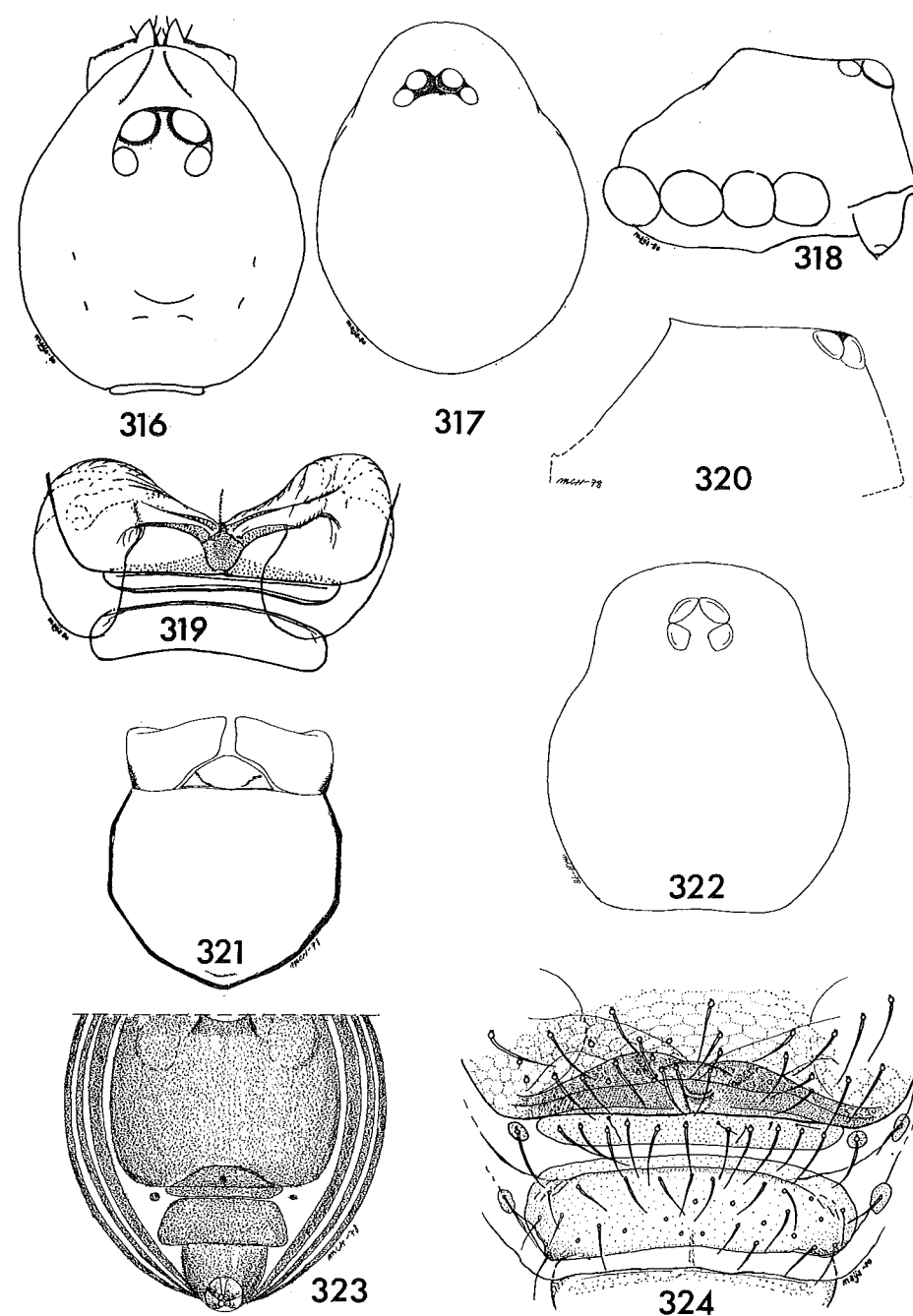
Figs 295—296. *Hexablemma cataphractum* Berland (holotype) (295), *Anansia astaroeth* (Brignoli) (296). — 295—296: cleared vulva.



Figs 297—308. *Matta hambletoni* Crosby (297, 300) *M. mckenziei* Shear (298, 301), *Caraimatta sbordonii* (Brignoli) (Vera Cruz, Volcan San Martin) (299, 304, 308), *C. blandini* sp. n. (holotype) (302, 305) and *Hexablemma cataphractum* Berland (holotype) (303, 306—307). — 297—299: male carapace and chelicerae dorsally. — 300—301, 304: male carapace and chelicerae laterally. — 302, 306: female carapace dorsally. — 305, 308: female carapace laterally. — 307: female abdomen ventrally.



Figs 309—315. *Hexablemma cataphractum* Berland (holotype) (309), *Caraimatta sbordonii* (Brignoli) (Veracruz, Volcan San Martin) (310, 315), *Matta mckenziei* Shear (311—313), and *M. hambletoni* Crosby (314). — 309: sternum. — 310, 312: female epigynal area and cleared vulva. — 311: male palpal cymbium. — 313: (a) male palp laterally and (b) apex of bulbus with embolus and conductor. — 314: male palp laterally. — 315: (a) male palp laterally and (b) apex of bulbus with embolus and conductor.



Figs 316—324. "*Monoblemma*" *muchmorei* Shear (316, 318), "*Monoblemma* ? *muchmorei*" (Virgin Islands, Angelica Rock) (317, 319), and *Maijana racki* sp. n. (320—324). — 316: male carapace and chelicerae dorsally. — 317: female carapace dorsally. — 318: male carapace and chelicerae laterally. — 319: epigynal area and cleared vulva. — 320: female carapace laterally. — 321: sternum. — 322: female carapace dorsally. — 323: female abdomen ventrally. — 324: epigynal area and cleared vulva (320—324: holotype).